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COMPARATIVE STUDIES IN THE GROWTH IN LENGTH OF LIMB BONES WITH SPECIAL REFERENCE TO THE UNION OF EPIPHYSES.

A thesis presented, together with reprints of other original papers, for the degree of Ph.D. of the University of Edinburgh by:-

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Introduction.

The object of this work is to study the long bones of the limbs in growing and grown up animals, specially of Class Mammalia; finding out any fundamental process underlying the difference in the epiphysial fusion and rate of growth of the limbs of animals of different orders; and in so doing to make a contribution to the problem of the growth of bones and to the role of epiphysis in that connection.

THE PROBLEMS OF BONE GROWTH:-

These have been ably summarized by Professor J. C. Brash[1] in his Struthers Lectures (1933) under three main heads;

1). The problem of the physiological, chemical, metabolic and perhaps mechanical control of bone development in relation to its ossification and increase or decrease in size;

2). The problem of the descriptive anatomy of the

the growth of bones in relation to the details of the sites and the balancing of the accretion and absorption of bone;

3). The problem of the means by which progressive ossification is controlled and guided, i.e. the "developmental mechanics", or, "developmental physiology" of bone.

These problems are essentially interdependent and their underlying processes fundamentally intimate, whether in physiological growth or pathological change. Leriche and Policard[2] recognised this and propounded that osteogenesis and osteolysis were interstitial phenomena controlled by circulatory variations independent of cellular action, osteogenesis taking place in connective tissues where fibroblasts happened to be present. According to them the idea that bone "is present to permit our movements" should be corrected, as bone is essentially a foreign body in relation to cells and must only be considered as a reserve of calcareous salts.

The problem of the developmental physiology of bone resolves into two queries, namely, (1) how far the form and structure of bone are determined by inherent genetic factors, and (2) how far they depend

upon

upon the mechanical circumstances of developmental environment. Recent experimental work by Murray and Huxley[3] and tissue culture methods of Fell and Robison[4] suggest that bones in the embryo are self-differentiating structures, every isolated fragment of which is totipotent and can produce the complete normal form without mechanical influence of its surroundings. Thus, the cause of bone development in the embryo and the differentiation of the primary form of individual bones depend on an inherent and therefore genetically determined factor. Such is also noted in the bone growth occurring apparently without any functional bias or mechanical stress in the well oriented exuberant bone growth in antlers of deer or in the excessive bone growth in the skull of the elephant or dugong. A high margin of safety for the delicate internal ear as present in the abundant layers of the temporal bone, and the appearance of air sinuses in the skull, where there can be no such argument of removal of support as is advanced for the tubulation of shafts of long bones, are further examples of the genetic factor. Further, mechanical stresses do not form any part in sclerosis

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of bone and the reduction of strength of a bone below safety limit in disorders of calcium metabolism. Our every day experience of the racial and familial facial resemblance, especially in uniovular twins, must depend upon inherited minute variations in the mode of growth of face bones.

Turning to the secondary ossification centres, Parsons' [5] 'traction', 'pressure' or 'atavistic' centre has no more than a descriptive significance. For Appleton[6] has shown that removal of gluteal musculature in rabbit has no effect on the ossification of its greater trochanter, proving a genetic factor for a 'traction' epiphysis.

The mechanical idea of the orientation of bone architecture according to functional needs was first suggested by Ward[7], elaborated by Meyer[8] and propounded as a Law by Wolff[9], viz. "Every change in the form and function of bones or of their function alone, is followed by certain definite changes in their internal architecture and equally definite secondary alterations in their external

configuration,

configuration, in accordance with mathematical laws". It is not known, however, how the functional orientation is brought about, except that controlled absorption of bone is the basic agency that brings about the modelling of its internal architecture, as well as its external form.

The fundamental problem of developmental mechanics is the control of absorption and not of accretion of bone, whether that control is vascular or cellular or both, acting from outside or inside.

THE MODE OF GROWTH OF LONG BONES.

Regarding this the following propositions may be taken as granted (Brash[1], Payton[10]).

1). The diaphyses of long bones grow in length by new bone replacing cartilage at their ends only, more being added at one end than at the other. On this, there are three sources of exact evidence:-

a). Experimental evidence by the classical methods of boring holes or fixation of artificial marks at measured distances apart in long bones of growing animals, as performed by Stephen Hales[11], Duhamel[12], John

John Hunter[13] and others. Krause's [14] experiments further showed that increments were unequal at the two ends of a rabbit's tibia;

b). Evidence by observation and measurement of bones. Payton[15], working on long bones of indirectly madder-fed pigs, has not only confirmed all the above findings and shown that greater increments occur at adjacent ends of femur and tibia, and at remote ends of humerus and radius, but has also given these facts an exact expression by measurement;

c). Evidence of radiographs of limb bones, confirming the belief that the mode of growth in length of human limbs is exactly similar to above, is provided by the observations of Harris[16], on the situation and relative position of transverse lines of denser shadow in radiographs at increasing ages of the same subject. These semi-permanent shadows appear at both ends of the bones and maintain their exact distance apart at increasing ages, but recede at unequal rates from the two ends.

2). Long bones grow in width by surface accretions. Surface or subperiosteal accretion of bone was first proved by Duhamel by fixing a ring of wire around the shaft of a growing bone. It is also beautifully shown in sections of madder specimens of any long bone. Goodsir[17], Macewen[18] and others maintain that osteoblast is the agent concerned in the process of surface accretion; Syme[19], Ollier[20] and others make the periosteum responsible for it; while Leriche and Policard explain it in the light of their own conception, viz., vascularity in connective tissues containing fibroblast.

3). Long bones maintain their shape by modelling

absorption

absorption principally towards their ends. Absorption also occurs within the shaft whereby the medullary cavity is increased and the tubular principle maintained upon which the shaft relies for its strength. Duhamel failed to explain why in his experiment the encircling ring apparently travelled towards marrow cavity. John Hunter explained the widening of marrow cavity as being due to absorption from within, and established the conception of "modelling absorption" as the means by which bones retain their shape as they grow in size. Bone growth and bone absorption are surface phenomena and they must go hand in hand in order that the characteristic shape of the bone may be maintained without altera tion or distortion. The knowledge of the mechanism of control of absorption in relation to accretion as an orderly purposive phenomenon in the sculpturing and re-arrangement of bone surfaces, may be the key to the main part of the whole problem.

The reverse picture of disturbance of modelling absorption at ends of long bones is seen in "diaphysial (Keith [21]) or metaphysial (Greig[22]) aclasia" as a symmetrical enlargement of the ends due to uncontrolled result of diaphysial growth in length (Hamann[23], Ingalls and Grossberg[24], Harris[25]).

4). Interestitial expansion of bone does not occur, bone growth being a surface phenomenon pure and simple.

5). No feature of a bone, however permanent it may seem, can be assumed as "fixed", for the purpose of comparison of different growth stages. The phenomenon of the growth of bones is associated with the "relativity of their form", since bones in general retain during their growth period those characteristic forms which were stamped upon them at an early stage

stage of their development, even before the earliest ossification began. While the corresponding parts of a bone at different stages of its growth stand in the same general relation to one another and to the bone as a whole, they are not the <u>same</u> parts, either in substance or position. Hence for the study of the individual "mode of growth" one must know, all the detailed features of its growth so as to be able to make any intelligent or sound comparison between different growth stages of the same bone, such as by way of superimposing one on the other in order to demonstrate real growth changes.

6). Stoppage of growth is marked by osseous union of epiphysis, absence of new formation of diaphysial bone and disappearance of absorption process controlling diaphysial new bone.

THE PROBLEM OF THE EPIPHYSIS.

An epiphysis may be defined as a mass of ossifiable (Todd & D'Errico[26]) cartilaginous complement found at the articular ends of a long bone, or at positions on it destined for muscular attachments or having no other than an 'atavistic' significance (Parsons). It was thought to be a bony cap, being, at least in many reptiles, partially of a 'sesamoid' origin though not a real sesamoid bone (Moodie[27]). It may remain as a separate piece in some animals, whereas in others it forms the component part of an adjacent bone.

Thus

Thus, in chiroptera, the olecranon epiphysis may remain as a distinct unit like the patella in the knee; in rats, the sternal epiphysis of clavicle may exist as a separate ossicle, the "praeclavium" (Dawson[28]).

<u>The genesis of the epiphysis:</u> This presents an interesting study. Haines[29] has shown that epiphyses do exist in bones of fishes and tetrapods. In fishes, it is seen as a mass of cartilage lying partly enclosed in the shaft of the adjacent bone and partly outside it. In the latter position the cartilage may have a secondary centre of ossification.

The first indication of preparation for articular epiphyses is found in lower Amphibia, Urodela and Discoglossidae (Parsons[5]). In these, ossification of shafts of long bones stops before it reaches articular ends and leaves a mass of cartilage which remains throughout life without either calcifying or ossifying. There is no epiphysis here but the place for it is provided. The curious thing is that most of these animals are aquatic. In the more specialised Anura - the higher frogs and toads - superficial calcification occurs in cartilaginous ends of bones when the animal is nearly or quite full-grown, and the calcified epiphysis fits over the diaphysis in the same way that the cover fits on to a pill-box. In Reptilia with limbs, articular

Fig. 1. Moni

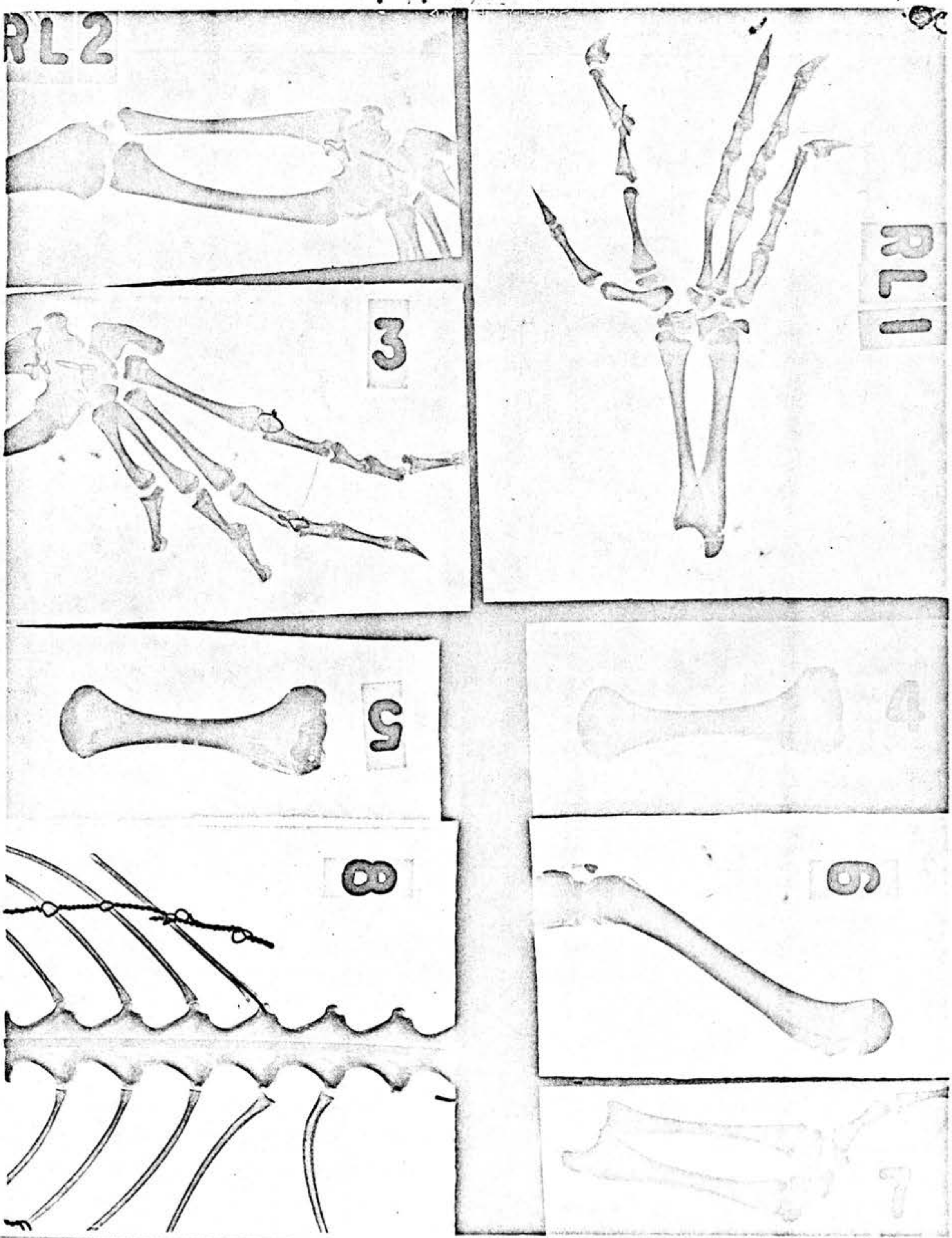

Fig. 1.

Radiographs of limb bones, vertebrae and ribs of a Varanus (from the Zoological Museum, Edinburgh University), showing flake-like calcification at ends of metacarpals, metatarsals and other limb bones. A distinct ulnar epiphysis is noticeable.

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Fig. 2. Ostrich

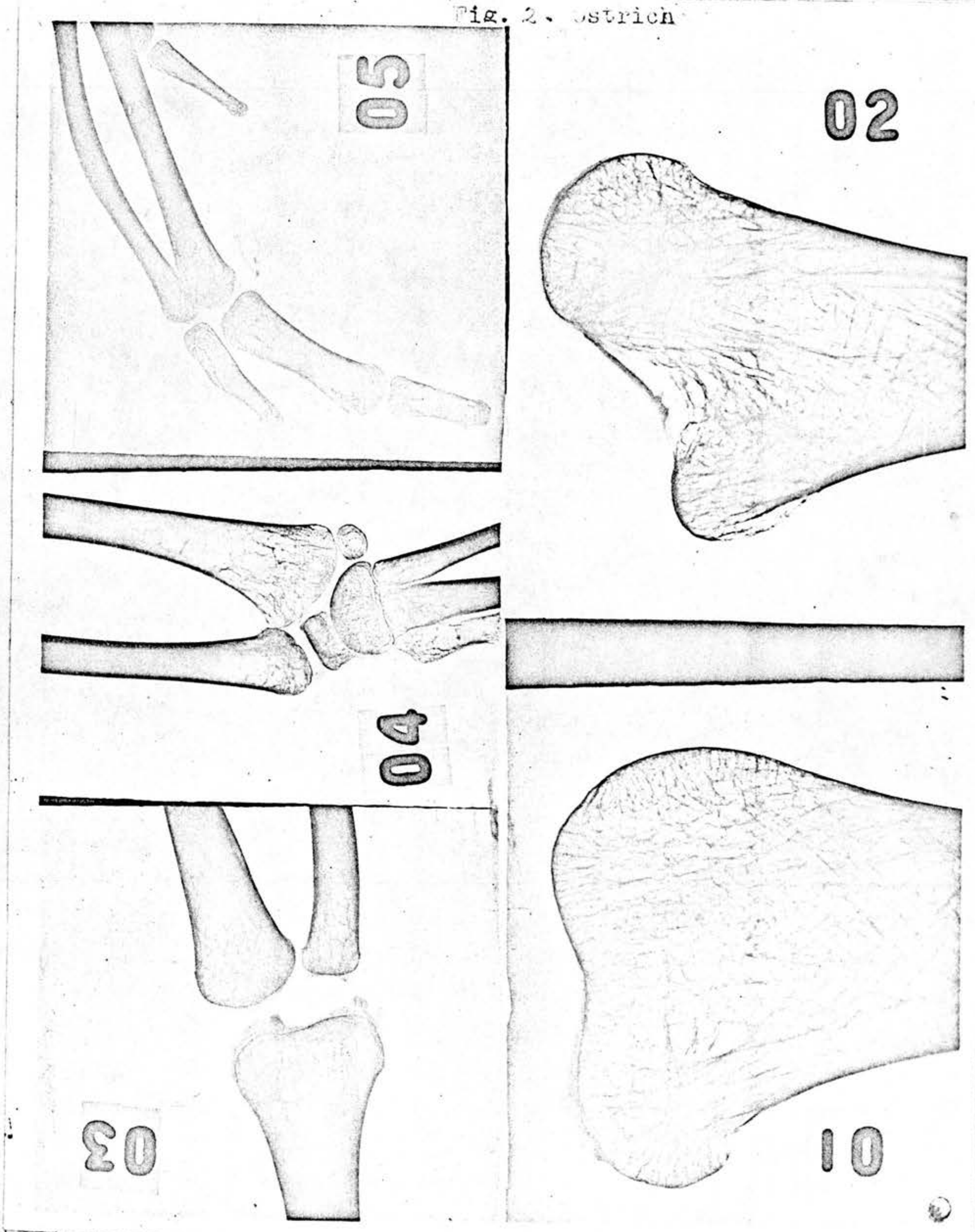

Fig. 2.

Radiographs of some of the limb bones from the skeleton of an ostrich (Zool. Museum, Edin. Univ.). No epiphysis is visible in any of the bones.

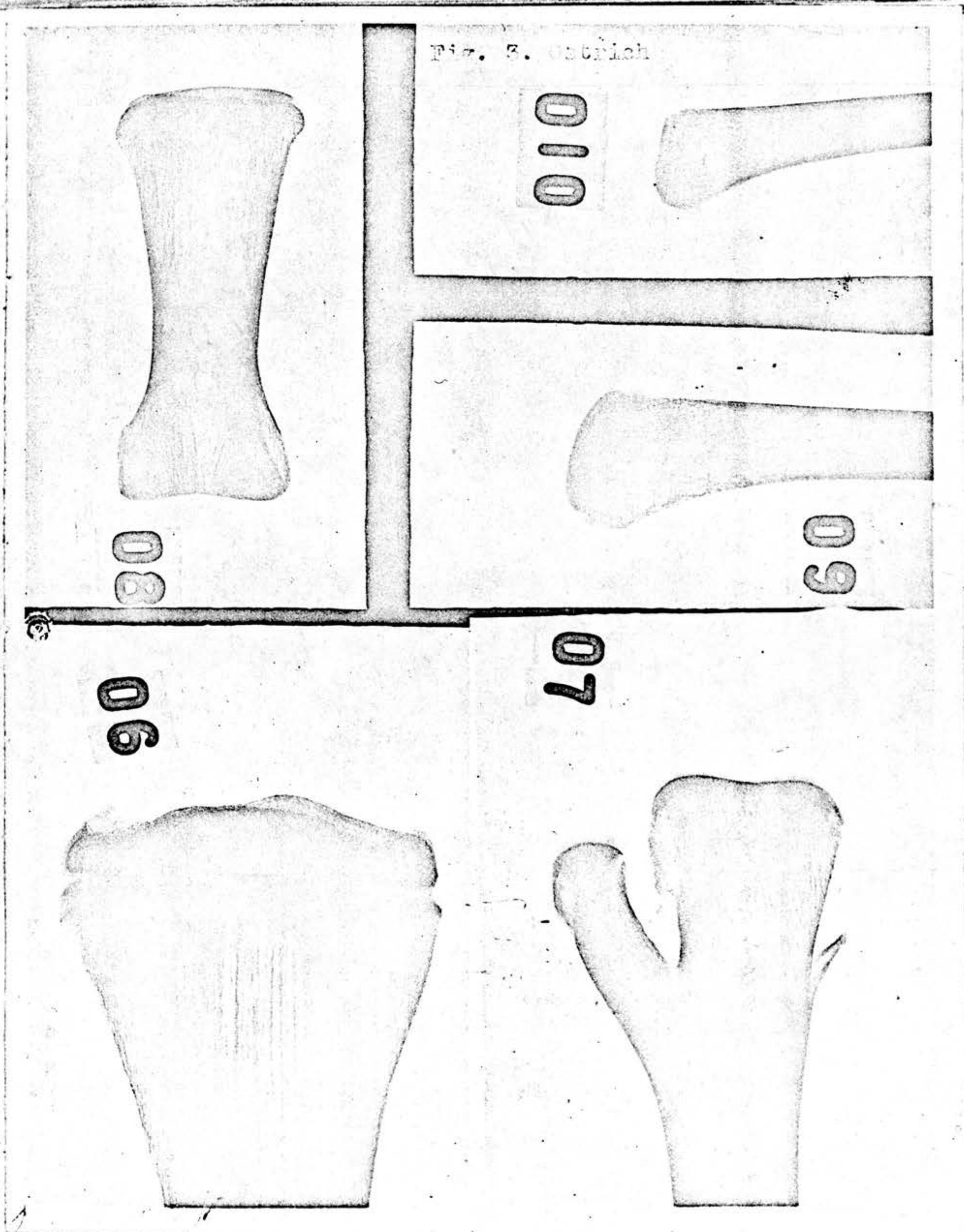

Fig. 3.
Radiographs of some of the limb bones of a bird (an ostrich skeleton from the Zool. Mus., Edin. Univ.), showing a true epiphysis at the proximal end of the tibio-tarsus.

epiphyses are fairly constant and many Lacertilia have epiphyses at both ends of their metacarpals and metatarsals and a definite articular epiphysis in the upper end of ulna. These epiphyses may be flake-like calcifications (varanus, Fig. 1) or ossifications (iguana). Birds are striking examples of the ease with which a bone can grow without epiphysis, there being only one instance of a true epiphysis at the upper end of tibio-tarsus (Figs. 2 & 3). This is probably a traction epiphysis (Parsons[5]), since it does not occupy the whole surface of the bone and since the ligamentum patellae is attached to it. Apart from this epiphysis in birds and certain reptiles, secondary centres of ossification in cartilaginous epiphyses are essentially mammalian features (Harris[25]). Further, it is seen that the higher the animal ascends in the scale of evolution, the more obligatory its relation with land, and the more completely it transfers the weight of its body on its limbs without aquatic or aerial support, the more well-marked and massive does the bony epiphysis become.

<u>The appearance of the epiphysis:</u> Parsons gives the following interesting account. Long bones of a series of pigeons 4 days to 6 weeks old show that (i) at 4 days, 2 cones of gradually ossifying cartilage, with apices close together at the point in the middle of the bone where primary

centre of ossification occurred, and with their bases quite unossified, form the articular ends; both cones are ensheathed by a layer of periosteal bone thickest opposite the apices of the cones and thinning off towards extremities; (ii) with age, ossification extends towards the bases of the cones, being for a short time checked at some little distance from the articular end; this is the equivalent of the epiphysial line of other vertebrates but is comparatively transitory and ossification creeps on until the articular end is reached, except for a narrow strip of articular cartilage; (iii) at six weeks, the bone has almost attained its adult dimensions, the apices of the cones, meanwhile, are gradually absorbed and replaced by marrow and air-sacs.

In terrestrial vertebrates, the epiphysial line or the place where the bases of the cones cease to ossify is much less transitory than in birds, and it retains its relative position to the articular ends. The area beyond it may remain cartilaginous (Urodela and Discoglossidae); may calcify, as in most Anura and many reptiles (chamaleon and monitor lizard); or may form the seat of a true epiphysis or osseous deposit, as in so many of the mammalia and in some reptiles.

<u>The role of the epiphysis:</u> "Epiphyses may be useful addition to a long bone, but they are not essential. In some

cases in mammals (ulna and clavicle in man), they appear so late in life that much or all of the growth of the bone has been effected without them. The possible uses of the epiphysis have been suggested as follows:-

1). They may assist in the growth of a bone. But this must be a very slight advantage, since growth is almost entirely on the diaphysial side of the epiphysial line. The ulna, which has no articular epiphysis in its upper end and a late appearing one below, keeps pace quite easily with the radius having epiphysis at both ends.

2). Deposit of bone beyond epiphysial line acts as a protection to the line of growth from stress or strain. But, for this, an elastic pad of cartilage must be better than a calcified or ossified area; and if any animal requires a protection against shock to the growing line of femur it must be the frog, yet no calcification occurs in it until growth is nearly complete.

3). By having a deposit of bone in the articular end, this end is able to adapt itself to change of shape which is constantly occurring during growth. This seems quite unnecessary, since everywhere bone is constantly being absorbed and relaid by osteoblasts and osteoclasts; and if any bone has a complicated articular extremity it is the mammalian ulna where it enters into the elbow joint; but this is the chief point where no articular epiphysis is found.

4). Attention is drawn to the fact that, in ungulates, epiphyses appear long before birth. Since these animals are able to run after their mothers almost as soon as they are born, it looks like a provision of Nature for a condition of things which would happen later on. But still it does not show what use the epiphyses are to the young animal. Some mechanical cause may in future be found for the early appearance of these ungulate epiphyses, showing how Nature can provide for some mechanical needs which have not yet arisen. It is quite certain that other animals can run about quite well while many of their bones still have their ends almost cartilaginous" (modified from Parsons[5]).

5). Broom[71] has supplied another hypothesis for the appearance of epiphyses. From his study of metacarpals and metatarsals in mammals, he concludes that, for long bones "those ends which took part in the formation of main joints would be the last to ossify and would determine the points where the epiphyses would form. The first carpal and first tarsal are so elongated that they might functionally be regarded as metacarpal or metatarsal (compare Orycteropus, Proboscoidea etc). Owing to this elongation the main joint of the first digit was between the carpal or tarsal and metacarpal or metatarsal, while in the case of other digits the most moveable joint was between the metacarpal or metatarsal and the first phalanx". Hence outer metacarpals or metatarsals would have epiphyses at distal end, but that of the first would be at the proximal end.

This theory however is very limited in its application and cannot explain why interphalangeal joints or the first metacarpo - or metatarso - phalangeal joints should not have epiphysis on all the bones forming them.

In the light of Appleton's experiments[6] it must be presumed that, whatever the origin or use of an epiphysis, the necessity for it was felt so much in the skeletal economy of the animal that a genetic factor had to be provided for it in the ultimate shaping of the bone.

<u>The transformation of the cartilages of epiphysis and diaphysis into bone:</u> Harris[25] maintains that "the most characteristic feature of cartilage is the specific limit of its growth in size by vegetative reproduction. This explains the order and pattern of the calcification and ossification of cartilage in the embryo, foetus and child. The same is true of a tuberculoma or gumma with their specific cells. Growth beyond this limit can only take place if senescence,

degeneration and death occur at the centre. This can only be avoided by the acquisition of a new irrigation system for the supply of nutrition to the centre. When a given mass of cartilage reaches the limit of size specific to the given site in any mammal, the central cells at the point of maximum nutritional disadvantage shrink, stain less definitely and calcification begins in the matrix. Hence the calcification of epiphyses starts once the limit of growth is reached. The narrow zone of epiphysial cartilage endowed with powers of prolonged growth, however, exhibits peculiar features. There is a normal rate of proliferation for cells of cartilage columns. There is, also a norm[illegible] in the number of cartilage cells in the column which is specific for each growth cartilage. Besides, such a limit is placed on the number of cartilage cells in the column that the cells at its diaphysial end, removed from the zone of activity, undergo senescence and degeneration, while the intervening matrix is calcified".

"The above processes result in what is virtually "dead" calcified cartilage and this is treated like a foreign body (vide also Leriche & Policard[2]) by the host. The calcified cartilage is attacked by an irruption of young actively growing capillaries from the adjoining marrow cavity or from the overlying perichondrium. The latter lays down ectochondral bone, and actively proliferating blood vessels erode the calcified cartilage and deposit endochondral bone" (Harris).

<u>Why epiphyses come:</u> That pressure, continuous or intermittent, can have no effect in starting calcification or ossification in bone has been shown by Parsons. From various considerations he concludes that epiphyses begin as a degenerative process in the least vascular part of the cartilaginous end of the bone, i.e. its centre. As mentioned above, the larger the mass of cartilage, the less well-nourished would the centre of it be and so the more liable to early deposit of lime salts. Hence the two main laws governing epiphysis, viz, (1) they appear in the centre of cartilage and (2) the larger the cartilage the earlier is the epiphysis to appear (Parsons[5]).

Ossification of diaphysis is checked at the future epiphysial line because the perichondrium is reflected off near articular ends to form the capsule of the joint and so the extremity is less well-nourished. The vessels supplying the diaphysis are derived from nutrient and medullary arteries which are end-arteries. The epiphysis is supplied by arteries supplying the capsules. Harris has shown that in positions like proximal ends of humerus and femur where reflection of capsules does not correspond with epiphysial line, muscles normally attached to the diaphysis, together with the capsular line, migrate from their primitive position on to the epiphyses or regress on the shaft, in accordance with the change of position and function of the primitive limb as it is made to adapt itself to altered conditions of existence and function.

<u>Morphology of Epiphysis in relation to function and limitation of growth:</u> Harris emphasizes that bony epiphyses have been evolved as a means of controlling or limiting growth. In reptiles and birds, the majority of the skeletal elements are preformed in cartilage which undergoes rapid calcification and ossification, with the exception of the cartilage pads which constitute the epiphyses. Compared with these forms the mammal is less precocious in development and this slowness of growth reaches its maximum in Man. This delay in the pattern of ossification is responsible for the persistence of outlying portions of cartilage in the skeleton, which subsequently ossify at their centres and eventually become ossified to the shafts of the bone. Thus the epiphyses have but little morphological significance. On the other hand, they have considerable functional significance, since the pattern of their development is so obviously related to retardation and limitation of growth and the time at which various physiological patterns are acquired. The earlier the functional importance of a part, the earlier does the secondary centre appear in it.

<u>The growth of the epiphysis:</u> The layer of actively proliferating cartilage intervening between the diaphysis and the epiphysis, the epiphysial or 'diaphysial'(Macewen[13]) cartilage, does not add to the growth of the epiphysis.

Fig. .

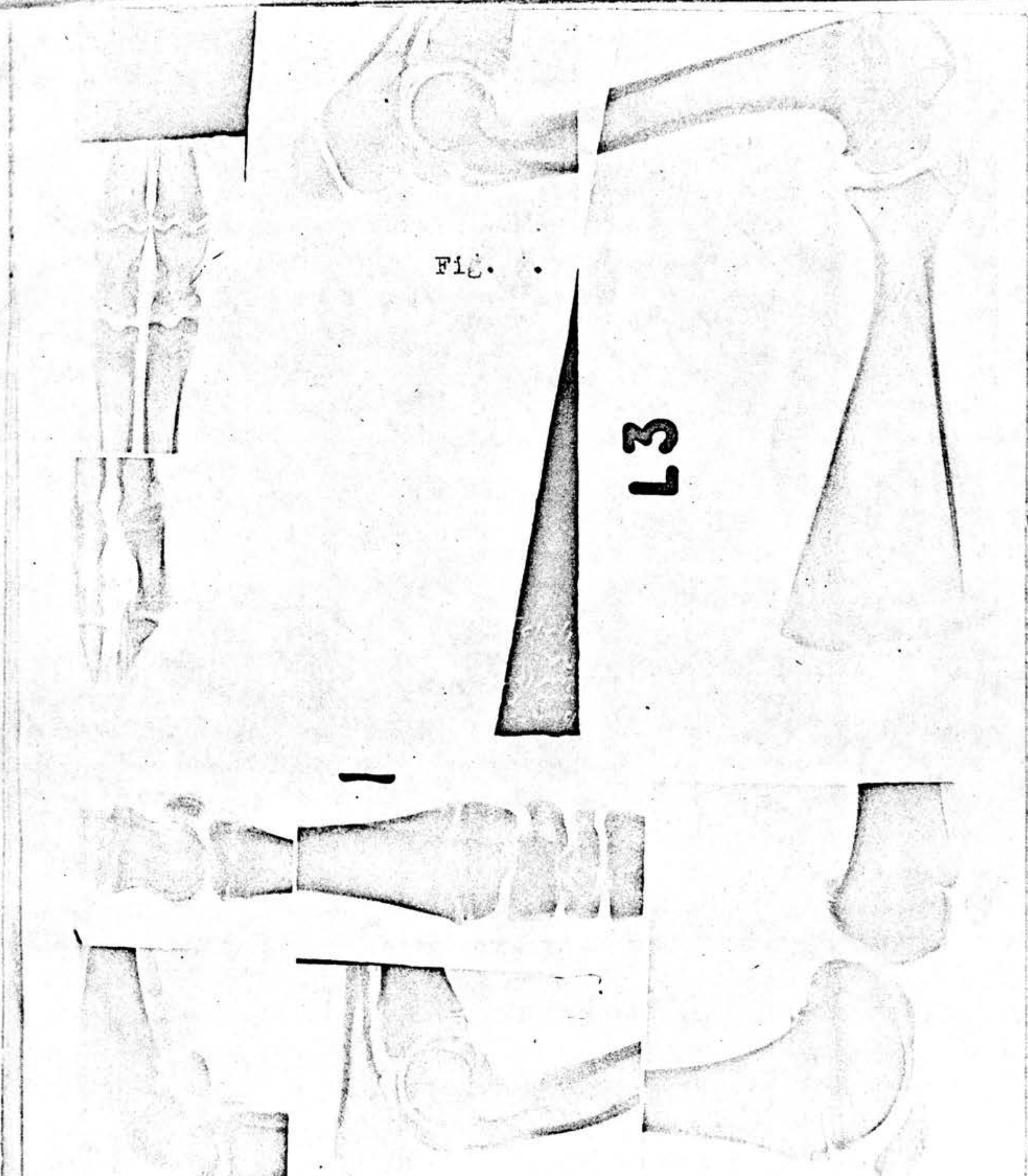

Fig. 4.

Radiographs of the unmacerated bones of a 16-day old antelope baby (from the Costorphine Zoological Gardens, Edinburgh), Showing absence of epiphysis at the terminal phalanges.

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Epiphyses, therefore, "do not grow on their diaphysial surfaces and the contribution that the epiphyses make to the total length of the bone depends entirely on additions to their joint surfaces beneath the articular cartilage" (Payton[10]). Further, "the increment on the articular surface of an epiphysis is considerably greater than its total increase in thickness" (Payton[30]).

The fate of the epiphysis (adapted from Todd literature, specially from Todd & D'Errico, Jr.[26] and Todd et al[31]). The precise composition of an epiphysis, whether fibrous tissue or cartilage, is immaterial. It may or may not ossify. By far the greater number of limb epiphyses ossify completely and unite over the entire surface of contact with the larger bone. There are certain epiphyses which sometimes ossify and sometimes do not, namely those of the second phalanges of the toes, in which ossification extending from the metaphysis gradually penetrates the epiphysis and ultimately leaves intact only the articular cartilage. Such epiphyses (showing no special centre and ossifying from the shaft) appear to unite when corresponding epiphyses, although ossified show no evidence of approaching union. Absence of special centres of ossification is probably an epiphysial regression (Francis & Werle[32]). A similar condition is seen in the terminal phalanges of fore and hind limbs of many ungulates and other animals (see Fig. 4). There are other epiphyses which regularly ossify only in part or patches, e.g., those of the clavicle and vertebral border of the scapula. In such cases the unossified part is absorbed but the differentiation and maturation between the part ossified and the shaft occurs as in the case where complete cartilaginous ossification has taken place (Todd[33]). Finally, there are epiphyses which ossify but never fuse with the corresponding shaft. This often happens in the case of distal radius and ulna, metacarpals and phalanges in many aquatic mammals, e.g., cetacea.

The problem of epiphysial fusion has always been a perplexing one. Burrows[34] has shown that 'archusia' and vitamin B acting in conjunction with 'ergusia' and vitamin A determine respectively the growth of primitive mesenchymal tissue and its functional differentiation into cartilage. Decrease in the activity of the former and increase in that of the latter leads to cessation of growth at the epiphysial line. An increase in Robison's[35] 'calcifying enzyme' at this stage brings on rapid calcification of matrix and degeneration of cartilage cells and is followed closely by ossification and epiphysial closure. Intensive study of 'growth' and other associated hormones has undoubtedly established the effect of an excess of or difficiency in certain internal secretions in the acceleration or retardation of epiphysial fusion (Evans[36], Smith[37], Dandy & Reichert[38]). The point, however, remains that normally the union of epiphysis occurs at definite sites and at a certain almost invariable age, and the body maturity runs pari passu with the epiphysial maturity (Outhouse and Mendel[39]). And the question arises, whether both of the above are self-determined processes predetermined in the bone (Rubinstein[40]) or whether they can be influenced by environmental factors. In the present work, an indirect proof has been given in support of the inherent nature of the process.

<u>Union of an epiphysis</u> (Todd literature) can only take place if ossification has occurred. Whether or not this has happened, there is a stage in the life history of the shaft when growth ceases. It means that an important stage of differentiation is terminated. This is usually the moment of epiphysial union, when the ossified epiphysis finally fuses with the shaft. It is common to all bony surfaces overlaid by an ununited epiphysis. Fusion of an epiphysis to shaft begins by narrowing of the sub-epiphysial space and approximation of neighbouring surfaces. The epiphysial surface of the shaft is finely granular and coral-like. Upon it are numerous depressions without apparent design. These are vascular in origin and disappear with the termination of growth at this site. Bony bridging-over commences at the centre and proceeds to the periphery, often with considerable

slowing down of the process just under the periosteum. Provided that the normal sequence of transformation occurs, all trace of distinction between epiphysis and major skeletal element disappears. But, if by any chance, some abnormal factor is at work, an epiphysial 'scar' may be seen temporarily or longer at the line of epiphysial union. This may be due to constitutional factors related to nutrition or diet or may have no particular significance.

The epiphysis, as it ossifies, becomes transformed into a bone of much closer texture totally unlike the surface of the shaft it is covering. This close and waxy texture is characteristic of an entirely quiescent bone, e.g. articular ends of bones, surface of cranial vault, face, neural arches of vertebrae, blades of scapulae, ossa innominata, greater part of carpals and tarsals, and those parts of long bones and ribs which are perfectly quiescent and undergoing no change whatsoever.

If, however, ossification has not occurred, or in sites where it is incomplete, the epiphysial cartilage disappears. The wrinkled and coral-like appearance that characterized the ossifying surface in an incomplete and earlier stage of ossification is replaced and the same waxy-textured bone which is typical of the epiphysis glazes over the naked end of the shaft. Such is often found in the sternal epiphysis of clavicle, the lesser trochanter of femur, the tubercle of tibia and the epicondyles of distal humerus and proximal ulna in some aquatic mammals (cetacea).

'Union of epiphysis' does not therefore imply the degree of ossification of the epiphysis but the loss of sub-epiphysial surface either by union of ossified epiphysis or by covering of sub-epiphysial surface by smooth-textured bone, an appearance which suggests as if candle-grease has been poured on the epiphysial site. This has been described by Todd as 'glazing'.

<u>Lapsed Union (Todd et al[31])</u> may occur in suture closure or at diaphysio-epiphysial planes. In man, it is most obvious at iliac crest and between bodies of the first and second sacral vertebrae. It is not delayed union which indicates possibility of ultimate fusion. The word 'lapsed' indicates that the impetus towards union is lost. It is a prohibition in the course of maturation which leaves the union permanently incomplete. Associated with this, changes, identifiable microscopically and with the naked eye, occur at the diaphysio-epiphysial junction. Lapsed union in ilium and sacrum is generally distributed through out mammalia. It is apt to be seen in distal radius and ulna in man and anthropoids. It is some times met with in head of humerus and femur especially in animals in captivity.

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In domestic animals it is seen at sites other than sacrum and ilium. It may be found without any ill-health or poor condition or improper or inadequate feeding (An 'eunuch' skeleton, offered for study by Prof. Brash at the Edinburgh University, showed this phenomenon at several sites). Specificity of the site of occurrence is curious, particularly in femur and humerus.

<u>Non-Union of epiphysis:</u> Union of some epiphysis at least never takes place in rodents, unless it may ultimately occur if they live long enough in natural conditions. Captivity interferes with the normal pattern of epiphysial union in time and sequence (Todd et al[31]).

<u>The sequence of epiphysial union</u> in different animals may be plotted for different stages and thus a pattern of fusion of the epiphysis in a definite order may be obtained, which is the 'epiphysial pattern' of the animal, as distinguished from its 'growth pattern' which implies change in bodily dimensions. The pattern is more or less the same for animals of the same group and differs slightly between families of any order. The sequence is unaffected to a large extent by nutritional, endocrinal or other generalized pathological disorders. But the whole process may be accelerated or retarded. Captivity and domestication have actually some, though little, influence in modifying the process. Fossorial and aquatic adaptations are rarely of

much significance. But the patterns differ in land and aquatic mammals (Todd et al).

Stevenson[41] proclaimed that "the sequence of epiphysial union in general is apparently constant throughout the entire range of land mammals" and the particular sequence of epiphysial union in man as brought out in his work is "not a specific, generic, familial or even ordinal characteristic, but that it may be considered a general mammalian trait and a true germinal character which is remarkably stable and very primitive." The same opinion has also been upheld by Todd and his school. A study of the sequence in different animals under various habitat, as revealed in the present work, disagrees in many respects with the views of Stevenson. It would rather seem to indicate that an environmental factor had, in the past, initiated certain definite sequence of union in the epiphyses, depending on the use and the stress and strain they were subjected to. Through millions of years of necessary repetition of the same sequence, a pattern of epiphysial union has been stamped on the gene of the particular type of skeleton which admits of little variation among members of one family but may be little or far removed from the pattern of other unrelated animals.

THE GENESIS AND SCOPE OF THE PRESENT STUDY.

The observations, recorded in the following pages, are the outcome of my work in the University of Edinburgh, during 1938 to 1940, under the direction of Prof. J. C. Brash of the Department of Anatomy, supplemented by further work, during 1940 to 1942, in different Institutions of U.S.A. and India. The study of the long bones of the limb in different animals was taken up, as stated before, to find out

i) how the fusion of epiphysis would stand in relation to the growth of the limb bones of different animals,

and

ii) whether the sequence of the fusion would be the same in all animals or vary according to their habitat, zoological position etc.

T H E   M A T E R I A L.

It consisted of :-

1). Dried osteological collections obtained from the galleries and bone-rooms of different Institutions of Great Britain, U.S.A. and India. Of the materials studied outside India, 130 skeletons were availed of at the Edinburgh University Anatomical Museum, through the generosity of Professor Brash. I am also indebted to Prof. James Ritchie for granting me facilities to study 94 specimens at the Zoology Department, University of Edinburgh; to Prof. T. Grahame of the Anatomy Department, Royal (Dick) Veterinary College, Edinburgh, for permission to examine 24 skeletons at his department; and to Dr.A. C. Stephen of the Royal Scottish Museum, Edinburgh, where 104 skeletons were studied. Through the introduction of Prof. Brash, Prof. W.K.Gregory of the Columbia University, N.Y., along with Drs. H.E. Anthony and J.E. Hill, very kindly helped me to examine 9~~3~~4 specimens in the Departments of Mammalogy and Comparative Anatomy at the American Museum of

Natural

Natural History, New York. A correspondence between Prof. Brash and Prof. N.L.Hoerr of the Western Reserve University, Cleveland, Ohio, enabled me to utilise the late Prof. Wingate Todd's admirably extensive collection of skeletal material in the Hamann Museum of Comparative Anatomy and Anthropology. I must express my great indebtedness to Prof.Hoerr for his generous permission to examine more than 392 skeletons from the wealth of material in the Hamann Museum and for the never failing help and hospitality of his laboratory. Through Prof.Hoerr and Prof.W. M. Krogman of the Department of Anthropology of the University of Chicago, I was introduced to Dr. C.Gregg, Director of the Field Museum, Chicago, where 33 specimens were very kindly placed at my disposal.

In India, 8~~0~~2 specimens were made available for study at the Indian Museum through the generosity of Dr. Baini Prashad and Dr. B. S. Guha, and 7 at the Department of Anatomy of the Carmiachael Medical College, Calcutta, through the kindness of my chief, Prof. M.N.Bose.

2).

TABLE No.1

List of Skeletons studied in different Museums.

Description of Animals	Edinburgh University Anatomical Museum	Edinburgh University Zoological Department Museum	Royal Scottish Museum Edinburgh	Royal (Dick) Veterin. College Museum, Edin.	Western Reserve Univ. Hamann Museum	American Museum of Natural History, N.Y.	Field Museum of Natural History, Chicago	Indian Museum, Calcutta	Carmichael Medical Coll. Anat. Museum, Calcutta	Total
Amphibia		1	1							2
Reptilia		7								7
Aves		10	1							11
Monotremata	2	4	2		2	4	1	1		16
Marsupialia	1	8	4	2	26	7	6	1		55
Edentata	1	4	4		8		22			39
Sirenia	3		1			5		1		10
Cetacea	19	1	3		1			5		29
Hyracoidea		1			6	5		1		13
Proboscoidea	2		1		2			3		8
" (Extinct)						3				3
Ungulata										
Artiodactyla	18+6	17	13	12	41			18		125
Perissodactyla	4	6	8		4			7		29
Carnivora	22	12	18	7	48			24		131
Pinnipedia	4		4		5			1		14
Rodentia	119	3	14	2	26	11		2		177
Insectivora	2	4	5		13	40				64
Chiroptera	1	4	4		1	9	3			22
Prosimiae (Lemuridae)	2	4	7		37	3		2	1	56
Primata (including Homo sapiens)	46	8	14	1	176	7	1	16	6	275
TOTAL	252	94	104	24	396	94	33	82	7	1086

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2). Carcasses of 6 recently born animals were received from the Costorphine Zoological Gardens, Edinburgh, and placed at my disposal by Prof. Brash for studying radiographic appearances of various epiphysial regions, with and without flesh, and after maceration.

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3). Skeletons of experimental animals as follows :-

i), 6 pigs and 49 albino rats from the madder and other colour-feeding experiments of Prof. Brash.

ii). 61 albino rats received from the Genetics Department, University of Edinburgh, and studied, at the instance of Prof. Brash, for Dr. Tang's work[42].

iii). 12 sheep (included in the list of animals studied in the Hamann Museum) used in the experiments of Liddell[43] and Simpson[44] at New York.

4). Radiographs of 135 Bengalee Girls from birth to maturity, which formed the subject of some of my previous papers[45].

The annexed table (Table No.1) shows a list of animals studied in the different Institutions.

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THE METHODS OF INVESTIGATION.

(A) The epiphysial condition of limb bones was recorded after examination mainly with the naked eye, assisted by magnifying glasses and, in the case of very small bones, by the dissecting microspope. The help of the X-rays had occasionally to be taken. The Hamann Museum offered exceptional facilities in this respect, since the late Prof. Wingate Todd had radiographed many of the doubtful areas of epiphysial fusion and carefully docketed the radiograms.

In assessing the amount of epiphysial union in dry skeletal material, the method of Stevenson[41] has been followed.

1). "The Stage of No Union" is referred to as ' — ' ; a clear hiatus existing, in radiograms, between epiphysis and diaphysis, and their approximated surfaces showing saw-tooth margins. At this stage an epiphysis may be entirely separated from the diaphysis in macerated bones, or separable on the slightest manipulation.

2). "The Stage of Beginning Union" is represented as 'B'. In radiograms, the tendency for the distinct

distinct hiatus is replaced by a line; the saw-tooth margins are gradually lost through deposition of fine granular new bone in the depressions; there may be an occasional bridging over or knitting together of the two margins, which process becomes increasingly conspicuous from this stage. In macerated bones, gentle manipulation fails to disengage the epiphysis from the diaphysis. The use of more force may separate them at the earlier stages of 'beginning union', showing the separated surface smoothed out by deposition of new bone as contrasted with the rugged surface of Stage (1). I have sometimes found it necessary to sub-divide this stage further into an earlier stage or 'B - ' and an advanced one or 'B + ' in order to allocate a chronological sequence to different epiphyses in animals of the same species, genus or family, that were at a similar epiphysial age.

3). 'The Stage of Recent Union', referred to as 'R', is the least definite of the four, being characterized by retention, in radiograms, of a fine line of demarcation, although the active process

of

of bony union is fairly over. It is seen best in freshly macerated skeletons as a line of faintly reddish colour. In old skeletons, bony trabeculae may be seen to be directly continuous from the diaphysis to the epiphysis with, may be, an occasional break here and there, or there may be an extremely faint break all round, which, at its bottom, shows the presence of perfect bony continuity from epiphysis to to diaphysis. These lines have to be distinguished from 'epiphysial scars' which, both in radiograms and macerated skeletons, are seen for a time even after complete epiphysial fusion.

4). 'The Stage of complete Union', referred as '+ ', is easy of recognition, though a faint epiphysial line may persist throughout life.

Stages (1) and (2) represent 'non-union' and (3) and (4) indicate 'union' , which are the two major conditions with their qualifying minor conditions. The actual age of union of epiphysis is the time when this significant transition between the major stages of absolute non-union and complete union takes place. This is why some authors, like A.H. Schultz[46 42], prefer referring to three stages of of union, as, (1) wide open ("W.O."), (2) Beginning Union ("B") and (3) Complete closure ("C.C"). Todd's description[47] of 9 stages of union and Hellman's[48] 5 stages are more applicable in finding out the exact data for detailed analyses of the adjacent contours of the bony epiphysial and diaphysial masses in a purely radiographic study in the living.

The eruption of teeth has been recorded in almost all cases and, wherever any doubt has arisen, a reference has been made to the closure of skull sutures. Dentition does not always have a harmonious relation with epiphysial fusion, but eruption of permanent molars is often helpful in arranging the skeletons in a chronological order. The condition of skull sutures is often useful for this purpose.

(B) The measurements of bones were carried out with sliding and spreading calipers, anthropometric rod, and osteo-metric board.

The maximum length of the clavicle was measured between its two ends; that of the humerus between its head and the inner border of trochlea; that of the radius, between the margin of its head and tip of styloid process; that

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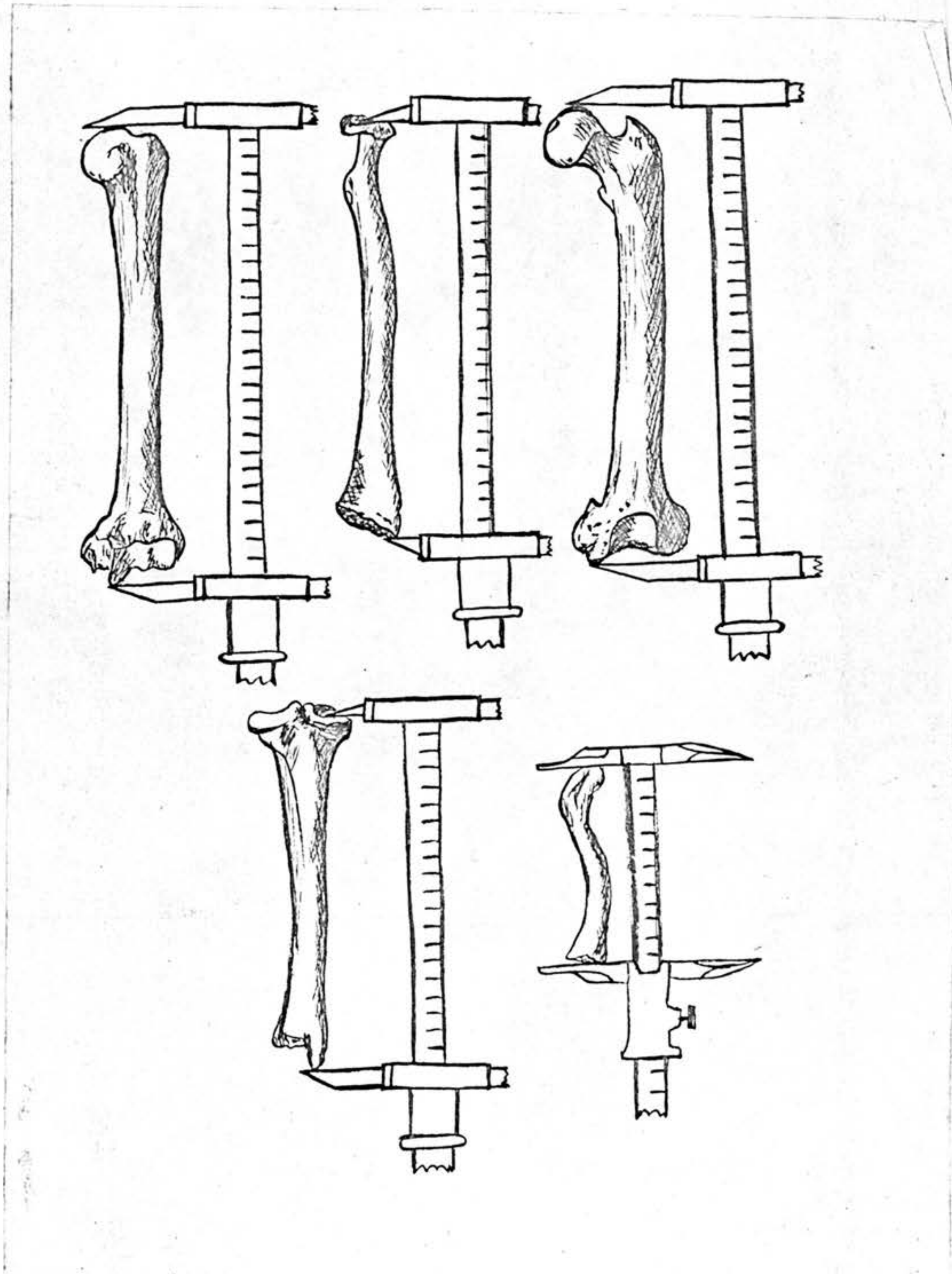

Fig. 35
Showing how measurements were taken
in some bones and the landmarks for the measurements.
(after A.H. Schultz).

[facing p. 32

that of the femur, between its head and medial-most margin of the medial condyle; that of the tibia between the margin of its medial condyle and the tip of its malleolus. The annexed drawings (Fig. 5) will tell their tale.

The measurements taken were to the nearest millimetre in bones of larger animals, and to the nearest half-millimetre in those of smaller ones.

From measurements taken as above the following indices have been calculated:

Brachial Index (RH) = $\frac{\text{Length Radius} \times 100}{\text{Length Humerus.}}$

Crural Index (TF) = $\frac{\text{Length Tibia} \times 100}{\text{Length Femur}}$

Humero-Femoral Index (HF) = $\frac{\text{Length Humerus} \times 100}{\text{Length Femur}}$

Inter-membral Index (IM) = $\frac{\text{Length Radius} + \text{Length Humerus} \times 100}{\text{Length Femur} + \text{Length Tibia}}$

The observations on epiphysial condition and the measurements of bones, in the living as well as in the dead material, were mostly taken on the right side, except when the right was damaged or inaccessible. Occasionally, for similar reasons, part of a limb of one side had to be

substituted

substituted by its counterpart from the other side. This was not of much importance in studying epiphysial sequence, since epiphysial condition remained almost similar at identical situations in both limbs. But it meant some slight deviation in the calculation of the indices, since the measurements of the same bone on either side seldom tallied exactly. In taking the measurements I was further handicapped in the case of specimens mounted in the old-fashioned way, as it was not possible to take them to pieces for fear of damaging them during the process of dismantling and reassembling. As a result, the exact landmarks for measurement were sometimes difficult to find. Some specimens in the galleries of the Anatomical and Zoological Museums of the University of Edinburgh, the Royal Scottish Museum and the Indian Museum were particularly deficient in this respect. Further, the estimation of epiphysial condition was also difficult in some of the gallery specimens where , for purposes of exhibiton, loose epiphyses were glued to the corresponding diaphyses, in the case of large animals; and, in smaller animals, they were either treated with an enamel varnish or with a coating of wax. In addition to being a relief to future workers, it would be of more educative value if taxidermists are instructed to bear the

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above difficulties in mind and make mounted preparations of skeletons from mature bones only, and articulate them in such a way that they can easily be taken down in pieces whenever required.

However, for my purpose, a series of observations had to be made in doubtful cases, assisted ~~with~~ by radiograms and more than one opinion of the readings, before a final result would be recorded. Inspite of all these, it is not impossible that a slight error here and there may have escaped detection but the amount cannot be large enough to deflect palpably the trend of the rest of the observations.

In the matter of measurements, the late Prof. Wingate Todd had been working at the shrinkage of bones in certain cases as a result of drying[74] ~~[45]~~,. It was not possible to get at dry and wet (unshrunk) skeletons of the various animals studied, the Hamann Museum being the only place where I could examine a few wet - preparations of anthropoid skeletons. The rest were all dried skeletons Marked shrinkage was observed in skeletons of very young animals where the bony epiphyses were still enveloped in a covering of cartilage. Measurements in such cases had

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mostly to be rejected, the epiphysial condition being the only thing noted. Many of the older collections in the different museums were evidently from menageric or zoo animals. The bones of such were often unacceptable for study and measurements, as they showed signs of malnutrition and deficiency diseases. Those showing slight deficiency were retained for partial study and a note has been inserted at the proper place.

The question of sex was not determinable in many of the specimens. Sex has been noted where possible.

Though the technical details of measurements of bones and the method of finding out their indices have been given in the previous pages, yet the actual figures have been omitted from the scope of the present work. The inquiry, whether the intra- or inter-membral proportions in the limb bones of the different animals would vary according to the functional adaptation of their limbs, is left over for a subsequent study.

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The present work may be taken up in two sections:-

Sec. I - The Study of Epiphysial Fusion. Pp.36-269

Sec. II - The Study of Epiphysial Fusion in relation to the growth of long bones. Pp.270-296

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SECTION I.

The Study of Epiphysial Fusion.

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ABBREVIATIONS.

Certain abbreviations have been used for convenience in the text and tables in this work.

As it is necessary to refer constantly to the several epiphyses studied, it has been found useful to give a number to each of them as indicated below:-

Number of epiphysis.	Abbreviation of epiphysis.	Full name of epiphysis.
1.	Clav, St.	Clavicle, Sternal end.
2.	Clav, Ac.	Clavicle, Acromial end.
3.	Hum, Pr. El.	Primary elements of proximal epiphysis of humerus.
4.	Hum, Pr.El. & Sh.	Fused primary elements of proximal epiphysis regarding fusion with shaft of humerus.
5.	Hum, Di.El.	Primary elements of distal epiphysis of humerus.
6.	Hum, Di.El. & Sh.	Fused primary elements of distal epiphysis regarding fusion with shaft of humerus.
7.	Hum, Lat. Ep.	Lateral epicondyle of humerus
8.	Hum, Med. Ep.	Medial epicondyle of humerus
9.	Rad, Prox.	Radius, proximal.
10.	Rad, Dist.	Radius, distal.
11.	Ulna, Prox.	Ulna, proximal.
12.	Ulna, Dist.	Ulna, distal.
13.	Mc, First	First metacarpal.
14.	Mc, Rest	Other metacarpals than first.
15.	Ph(M), Prox.	Proximal phalanx of manus.
16.	Ph(M), Mid.	Middle phalanx of manus.
17.	Ph(M), Term.	Terminal phalanx of manus.
18.	Fem, Head	Head of femur.
19.	Fem, Gr.Tr.	Greater trochanter of femur.
20.	Fem, Ls.Tr.	Lesser trochanter of femur.
21.	Fem, Dist.	Femur, distal.
22.	Tib, Con.	Tibia, condyles.
23.	Tib, Tb.	Tibia, tubercle.
24.	Tib, Dist.	Tibia, distal.
25.	Fib, Prox.	Fibula, proximal.
26.	Fib, Dist.	Fibula, distal.
27.	Calc, Epip.	Calcaneal epiphysis.
28.	Mt, First	First metatarsal.
29.	Mt, Rest	Other metatarsals than first
30.	Ph(p), Prox.	Proximal phalanx of pes.
31.	Ph(P), Mid.	Middle phalanx of pes.
32.	PH(P), Term.	Terminal phalanx of pes.
33.	Ext. Centre	Extra centre or centres.

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ABBREVIATIONS OF EPIPHYSIAL CONDITION.

Abbreviation.	Full name.
A or Act.	Active.
Abs.	Absent.
Q	Quiescent.
B	Stage of beginning union.
B-	Stage when union is just beginning.
B+	Advanced stage of B, almost nearing completion of union.
Ct. or cart.	(in) cartilage.
F	Fused.
G or Gl.	Glazed.
L.U.	Lapsed union.
M	Missing
nil	Epiphysis or the part is absent.
R	Stage of recent union.
S.H.	Study is handicapped owing to the epiphysis being fragmentary or covered by ligament or wax or the portion could not be dismantled or closely inspected.
-	Stage of complete non-union.
+	Stage of complete union.
?	Either the study is incomplete due to absence of an epiphys. or the stage of epiphysial activity is in doubt.

ABBREVIATIONS FOR MUSEUMS ETC.

A.M.N.H.	American Museum of Natural History, New York, U.S.A.
B.C., I etc., 1,2 etc.	Basement cupboard, No.I etc., Shelf No.1, 2 etc.
B.R.	Bone Room.
C	Case.
C.M.C.	Carmichael Medical College (Calcutta) Anatomical Museum.
E.U.A.	Edinburgh University Anatomical Museum.
E.U.Z.	Edinburgh University Zoological Dept. Museum.
F.M.	Field Museum of Natural History, Chicago, U.S.A.
Gal.	Gallery.
I.M.	Indian Museum, Calcutta.
m.g.	Mammal gallery of the Indian Museum.
R.D.V.C.	Royal (Dick) Veterinary College (Edinburgh) Anatomical Museum.
R.S.	Royal Scottish Museum, Edinburgh.
S.m.g.	Small mammal gallery, Indian Museum.
W.R.U.	Hamann Museum of the Western Reserve University, Cleveland, Ohio, U.S.A.

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OTHER ABBREVIATIONS.

Abbreviation.	Full name.
Abs.	Absent.
Ac.	Acromion or Acromial.
Basil	Basilar suture.
Calc.	Calcaneal.
Clav.	Clavicle.
Con.	Condyle.
Coron	Coronal suture.
Ct. or cart.	Cartilage.
Dist.	Distal.
El. or Elem.	Elements.
Ep. or Epip.	Epiphysis.
Epic.	Epicondyle.
E.U.S.	Sequence of epiphysial union.
Ext.	Extra or external.
Fam.	Family.
Fem.	Femur.
Fib.	Fibula.
Gen.	Genus.
Gr.	Greater.
Hum.	Humerus.
Lat.	Lateral.
Lig. or Ligt. or Ligam.	Ligament or Ligamentous.
Ls.	Lesser.
Lt.	Left. -
M	Missing.
Mc 1,2,etc., r	Metacarpal, first, second, etc., rest.
Mt 1,2,etc., r	Metatarsal, first, second, etc., rest.
Mid.	Middle.
nil	Not found or done.
Ord.	Order.
Ph(m) 1 etc.	First etc. phalanx of manus.
Ph(p) 1 etc.	First etc. phalanx of pes.
Pr. or Prox.	Proximal.
Prim.	Primary.
Rad.	Radius.
Rt.	Right
Rud.	Rudimentary.
S.F. or S. Fam.	Sub-family.
Sh.	Shaft.
S. Ord. or S.O.	Sub-order.
Sec.	Section.
Seq.	Sequence.
Skel.	Skeleton.
Sp. or Spl.	Special.
St.	Sternal.
Sut.	Suture.

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Abbreviation.	Full name.
T	Tongue-shaped projection.
Tb. or Tub.	Tubercle or Tuberosity.
Term.	Terminal.
Tib.	Tibia.
Tr.	Trochanter.
Ul. or Uln.	Ulna.
Var.	Varnished.
x	Absent or not found or not studied.
?	Doubtful.

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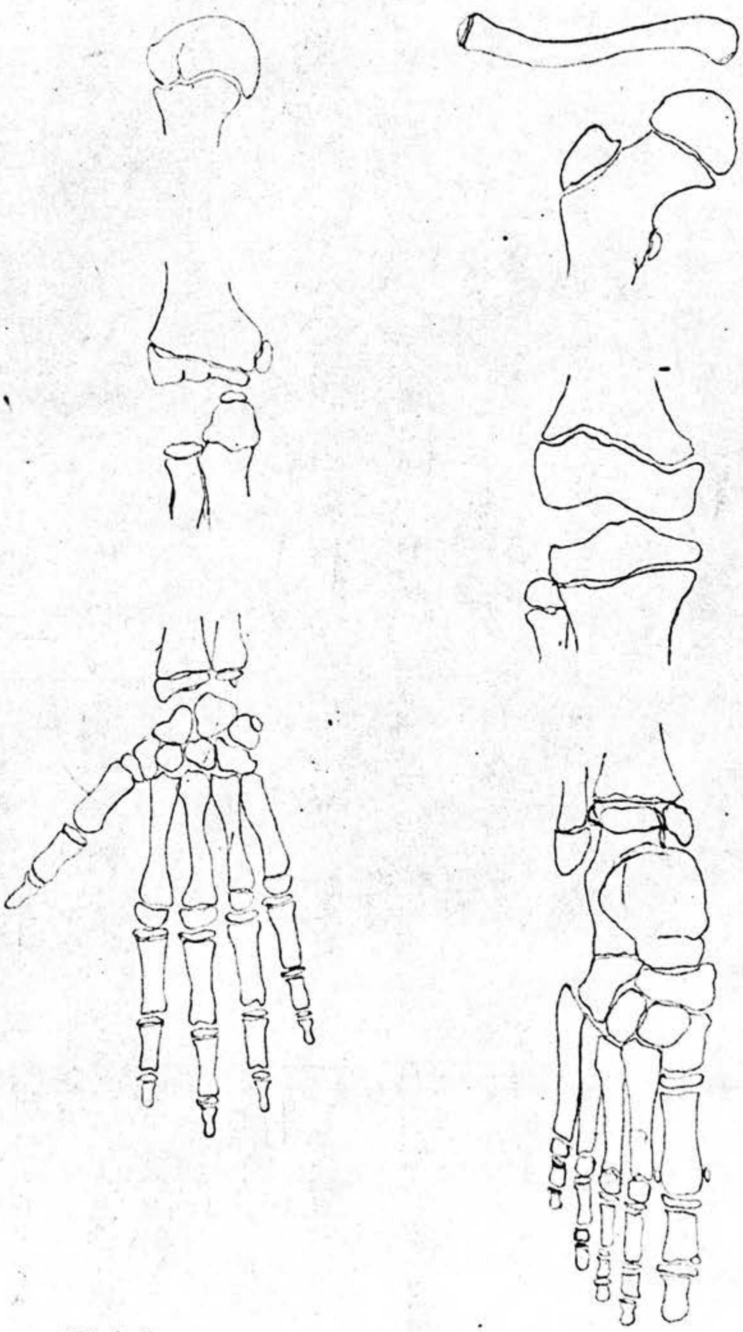

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Fig. 6.

Diagrams showing the epiphysial positions in the limb bones of man.

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THE FUNDAMENTALS IN THE STUDY OF LIMB EPIPHYSES.

Two types of epiphyses are usually found in the long bones of the limbs, the articular or 'pressure' epiphyses which by their fusion with the shaft stop the growth of the bone, and the non-articular or 'traction' epiphyses associated with the pull of muscles. The latter have something of the nature of sesamoid bones (Parsons[5]).

The position and the number of epiphyses are roughly the same in the limbs of all land mammals. The standard may be taken from those found in man. The annexed diagrams (Fig. 6) will explain their purpose.

Clavicle: One epiphysis at either end. Some Anatomists do not admit the existence of an epiphysis at the acromial end of the human clavicle. Todd & D'Errico hold that there is rarely an ossification in the lateral epiphysis of clavicle. A bony nodule does often develop in this epiphysis, but it is often rudimentary and its fusion with shaft is very rapid. "Should there be no bony nodule developed, the epiphysial cartilage disappears and the end of the shaft becomes glazed over with a waxy textured bone, simulating a united epiphysis". Hence it is often difficult to assign the stage of union of clavicular epiphyses. The symbols of 'A' (active) and 'Q' (quiescent) therefore have often been used for these instead of 'B' or

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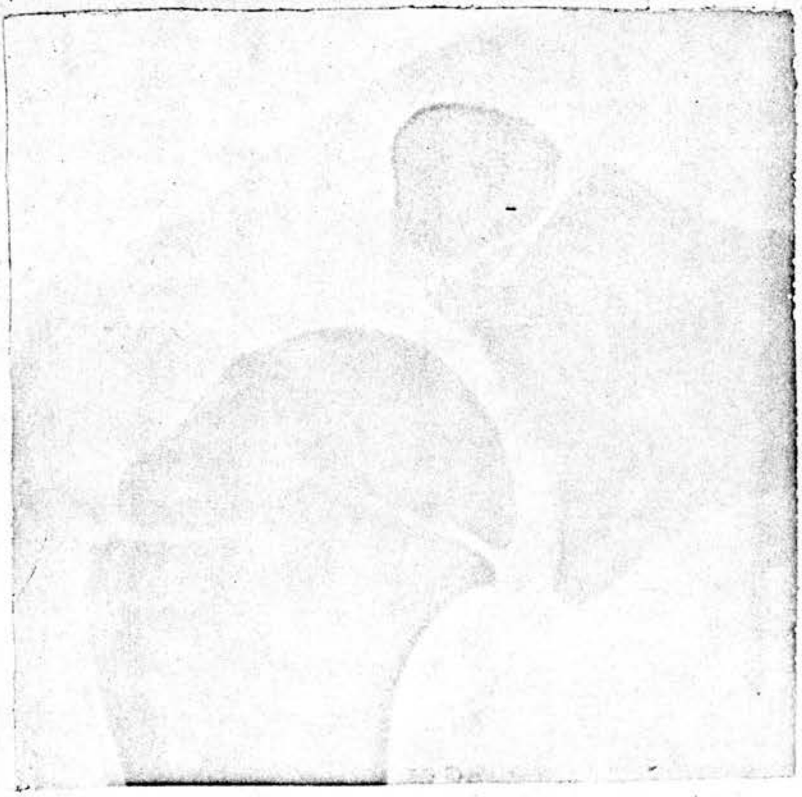

Fig. 7.
Radiograph of the carcass of a new-born camel (from the Costorphine Zoo, Edin.), showing the shoulder-joint. The head of the humerus is showing three distinct epiphysial centres.

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'+' as in other epiphyses. Doubtful cases have been shown as '?' or 'x'.

<u>Humerus</u>: Anatomists recognize the presence of three primary elements in the proximal end. "Radiograms show a separate centre for the greater tuberosity in only 50% cases (Paterson[50]), and seldom show one for the lesser tuberosity; and though the overlap of shadows may account for their apparent absence in some cases, yet it may be that the tuberosities are often ossified by extensions from the head" (Cunningham [49]). In Monotremata, some Insectivora and others (to be referred later) the elements do not fuse together as in man and most other mammals. The presence of three different elements has been observed in many young mammals. The annexed radiograph (Fig. 7) of a new born camel examined at E.U.A. shows them up.

The distal epiphysis is composed mainly of two epiphyses, capitulum and trochlea, and an epicondylar epiphysis on each side. The lateral epicondyle in man "usually joins the shaft independently (Paterson), but it may fuse with the capitulum before doing so"; and in 25% to "30% of cases it appears to have no separate centre" but is a tongue-like projection from the capitulum(Paterson[50], Galstaun[51], Basu & Basu[45]). The medial epicondyle in man unites only with the shaft of humerus, but in various lower

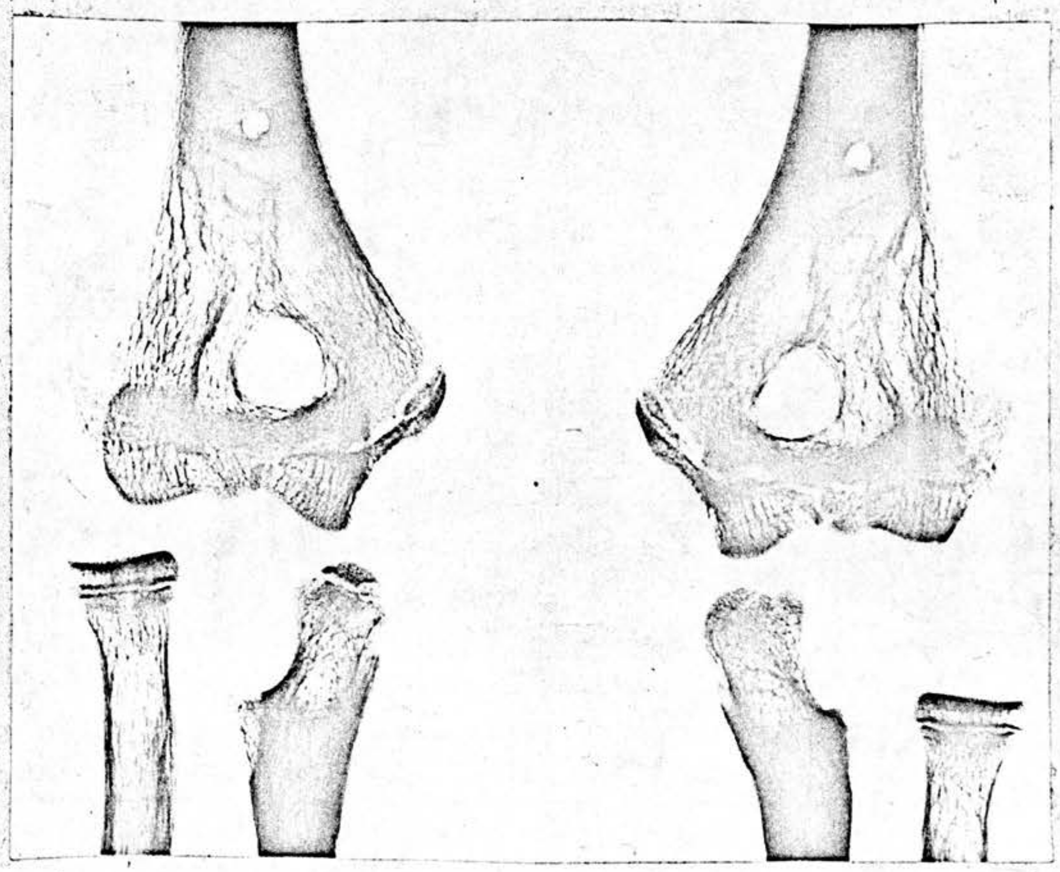

Fig.8.
Radiograph of the bones at the elbow of an Orang-utan skeleton (No. B625 in the Hamann Museum of the Western Reserve University, Cleveland, Ohio, U.S.A.), showing union of epiphysis for medial epicondyle with both trochlear epiphysis and shaft of humerus.

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animals it unites with the trochlea as well (see Fig. 8).

Radius: The proximal and distal epiphyses are always present except in Cetacea, where it seems that there is a sub-cartilaginous ossification for the proximal end without the presence of a so-called epiphysis and there may be no epiphysis for its distal end.

Ulna: The olecranon and distal epiphyses are always present, except where the distal end is reduced, as in some ungulates, bats etc. They may be vestigial or absent in aquatic mammals.

Metacarpals: Usually five, but the number may be reduced and there may be a pre-pollex. Pollex has an epiphysis at base, the others at the distal end. Metacarpals of aquatic mammals have an epiphysis at each end which, in cetacea, do not unite with the shaft. Extra epiphysis may be present at the base of one or more of the outer metacarpals in land mammals. In some Ungulata the metacarpals form a 'cannon'.

Phalanges: Normally there are three phalanges to each metacarpal except the pollex which has two. Each phalanx has an epiphysis at base except in the ungual phalanx (?) in some ungulates etc. The number of phalanges may be increased (Cetacea) with an epiphysis at each end (except the terminal phalanx), which does not unite. The number may be reduced or some of the epiphyses may be absent, as in bats.

Femur: Proximally the head and greater trochanter

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are present in all animals having a functional hind limb. The lesser trochanter may be distinct or may have a non-epiphysial ossification characterized by 'glazing'. The distal epiphysis is present in all mammals having a femur.

Tibia: Proximally the condyle is always to be found. The tubercle may be present as a separate epiphysis or a tongue-like projection from the condyle. The distal epiphysis is always present.

Fibula may be absent or reduced (Ungulates, Chiroptera etc.). Usually, it has an epiphysis proximally, which provides articulation with Tibia. In Monotremata the proximal end is bifurcated, each arm bearing an epiphysis. The proximal epiphysis may be absent owing to reduction of this end of the bone, as in bats. The distal end has an epiphysis, unless it be ankylosed (some rodents). In ruminants, the fibula is represented only by the lower end (malleolar bone).

Tarsals: The calcaneus almost always has an epiphysis (apophysis). The navicular may have one.. The calcaneus and navicular in some lemurs (Tarsius, Galago etc) are extraordinarily elongated.

Metatarsals: Similar to metacarpals. There may be a pre-hallux. The fifth may have an epiphysis at either end. Some metatarsals may be elongated as in some insectivores (Macroscelididae) and rodents (Dipodidae) or form 'cannon' as

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Table No.2

Ages of Union of Epiphyses as assigned by various Anatomical Authorities before Stevenson (modified from Stevenson)

	Humerus			Radius		Ulna		Femur				Tibia		Fibula		
Authority Year	Head.	Dist.Ex	Med.Ep.	Prox.	Dist.	Prox.	Dist.	Head	Ls.Tr.	Gr.Tr.	Dist.Ex	Prox.	Dist.	Prox.	Dist.	Clavicle
Bryce (1911)	20-22	17	18	17-19	18-20	17-19	18-20	18-19	18	17	20	19-24	17-19	22-24	20-22	25
Cunningham[52] (1922)	25	16-17	16-17	18	21	17	21	18-20	18	18-20	21	21	18	18-20	18-20	22-25
Dixon (1912)	20-25	17	18	18	21-25	17	20	18-20	18	18	23-24	21	17-18	22-24	20	25
Dwight (1911)	20	15	-	16	19-20	16	18	18	19	19	20	21	17-18	22-24	20	25
Gegenbaur (1892)	-	18	-	17	20	17	20	20-25	20-25	20-25	23	-	-	-	-	-
Henle (1871)	-	15	16	16	19-20	15-16	20	20	-	-	-	18-25	18-25	19-25	19-25	18
Krause (1909)	22	16-17	18	16-17	20-21	16-17	20-21	17-19	17-19	17-19	19-20	19	17-18	19	17-18	20-22
Lewis (1918)	20	17	18	17-18	20	16	20	Puberty to			20	20	18	25	20	25
Morris[53] (1914)	20-21	17	17	17-18	20	17	20	19	17	18	20	21-25	18	22	20	22-25
Piersol[54] (1918)	20-21	17	17	17-19	18-20	17	20	18	19	19	20	19-20	18	20	18-19	25
Poirier (1911)	20-25	16-17	16-17	16-19	20-25	20-21	22-24	18-22	18-22	18-22	20-24	18-24	16-18	22-23	20-22	25
Terry (1921)	20	17	17	17	20	16-17	18-20	19	17	18	20	20-25	18	22	20	25
Testut (1921)	20-25	16-18	17-19	16-20	20-25	16-20	20-25	18	18	16-18	20-22	18-20	16-18	19-22	18-19	22-25
Thompson (1921)	25	16-17	18-19	18-20	20-25	16	20-23	18-20	18	18-19	20-22	20-24	18	19	19	25
Earliest	20	15	16	16	18	15	18	18	17	16	19	18	16	18	17	18
Latest	25	18	19	20	25	21	25	25	25	25	24	25	25	25	25	25
Difference	5	3	3	4	7	6	7	7	8	9	5	7	9	7	8	7

much worn Much worn
other dec.

M^1

1

in ungulates.

<u>Phalanges</u>: Similar to those of the fore-limb. The epiphysis for second phalanx of some toes may not develop a centre of ossification (Todd[31]). Frequently second and third phalanges of 5th toe fuse to form one bone (Francis & Werle[32]).

Occasionally there may be extra centres and bones not indicated in the foregoing account.

THE STUDY OF EPIPHYSIS IN MAN.

The study of epiphysis in man was irregular in the days preceding the work of Stevenson. Table No.2 (modified from Stevenson[41]) gives the dates of epiphysial union as given by earlier anatomists. It also gives the earliest and latest ages of union of epiphysis and the difference in the timings. A study of the table shows that it would be difficult to make out an exact sequence of epiphysial fusion since the range of the latter extends over a period of 3 to 9 years. Stevenson solved this difficulty after a comprehensive study of 110 age-known and well-identified skeletons in the Hamann Museum. The sequence as worked out by him is shown in Table No.3.

Table No.3

Sequence of Ep. Union in limb bones of Man
(Stevenson)

Distal extremity of humerus
(Medial epicondyle of humerus)
Head of radius
(Olecranon of ulna)
Head of femur
(Lesser and greater trochanters of femur)
Distal extremities of tibia and fibula
Proximal extremity of tibia
(Proximal extremity of fibula)
Distal extremity of femur
Distal extremities of radius and ulna
Head of humerus
Clavicle

Medial epicondyle humerus, olecranon, trochanters of femur and proximal fibula are inconstant in their behaviour and should not receive much emphasis in epiphysial charts.

There has been a good deal of radiographical work on the epiphysis of living human beings, a few preceding the publication of Stevenson's work but, most of them appearing later. A change is also being noticed in the timings given in more recent text books. Table No.4 shows a few of such timings against those given in Table No.2. It will be seen that the long ranges of difference in the earliest and latest ages for the union of epiphysis have been appreciably shortened in later works.

Table Nos.5 & 6 show the result of some of the vast radiographic works on epiphysial union in man. Here also the difference in age between the earliest and latest times of

Table No.4

Ages of Union of Epiphyses as assigned by Stevenson and later Anatomical Authorities.

Autho-rity Year	Humerus			Radius		Ulna		Femur				Tibia		Fibula		
	Head.	Dist.Ex.	Med.Ep.	Prox.	Dist.	Prox.	Dist.	Head.	Ls.Tr.	Gr.Tr.	Dist.Ex.	Prox.	Dist.	Prox.	Dist.	Clavicle.
Stevenson[41] (1924)	20	15	16	18	19	16-17	19	Early 18			19	18-19	18	18-19	18	28
Frazer[55] (1933)	18-20	14-17	15-18	14-17	17-19	14-17	17-19	17-18	17-18	17-18	17-19	17-20	16-18	17-20	16-18	20
Gray[56] (1935)	20	16-17	18	17-18	20	16	20	After puberty			20	20	18	25	20	25
Cunning-ham[49] (1937) M	21	19	18-21	18-19	21	18-19	21	18	18	18	18	18-19	18	18	18	25
F	18	14-15	14-15	14-15	19-20	14-15	19 20	17	16-17	16-17	16-17	16-17	16	16	16	25
Earliest	18	14	14	14	17	14	17	17	16	16	16	16	16	16	16	20
Latest	21	19	21	19	21	19	21	18	18	18	20	20	18	25	20	28
Difference	3	5	7	5	4	5	4	1	2	2	4	4	2	9	4	8

much worn Much worn
other dec.

M^1_-

1

Table No.5.
Age of Union of Epiphyses as assigned Radiographically in different countries.

Authority Year.		Humerus. Head.	Dist. Ex.	Med.Ep.	Radius. Prox.	Dist.	Ulna Prox.	Dist.	Femur. Head.	Ls.Tr.	Gr.Tr.	Dist. Ex.	Tibia. Prox.	Dist.	Fibula Prox.	Dist.	Clav. St.end	Ac.end
AMERICAN																		
Engelbach & McMahon[61] (1924)	M	18	16		16	17	16	18-20	18	18	17	18-20	18-20	18	18-20	18-20	22-25	
Holmes & Ruggles[58] (1931)	M & F	18	17	18	17	18	17	18	19	18	17	20	22	18	24	20	25	
Pillsbury[59] (1932)	M & F	20	15-17	19	16-18	20	17	20	18-19	18	17	20-21	19-22	17-19	19-24	19-21	25	
Prøyor[57] (1908-30)	M	-	-	-	-	-	-	19	-	-	-	-	-	-	-	-	-	-
	F	-	-	-	-	-	-	16	--	-	-	-	-	-	-	-	-	-
Todd[47] (1929-30)	M	19½-20½	14-15	15-16	14½-15½	18-19	14½-15½	18-19	17-18	17-18	17-18	17½-18½	17½-18½	15½-16½	17½-18½	15½-16½	25-28	19-20
	F	19½-20½	12½-13½	13½-14½	12½-13½	18-19	12½-13½	18-19	17-18	17-18	17-18	17½-18½	17½-18½	14½-15½	17½-18½	14½-15½	25-28	19-20
Todd[73] (1933)	M	19.6-20.5	14.0-14.11	15.6-15.11	15.0-15.11	-	14.6-15.5	18.0-18.11	17.0-17.11	17.0-17.11	-	18.0-18.11	17.6-18.5	15.6-16.5	17.6-18.5	15.6-16.5	-	-
	F	19.0-20.0	12.6-13.5	13.6-14.5	12.6-13.5	-	12.6-13.5	18.0-18.11	17.0-17.11	17.0-17.11	-	17.6-18.5	17.6-18.5	14.6-15.5	17.6-18.5	14.6-15.5	-	-
AUSTRALIAN																		
Flecker[60] (1932)	M	19	16	16	16	19	16	18	17	17	-	19	18	17	19	17	22	-
	F	17	13	15	14	18	14	17	14	14	-	17	15	14	17	14	22	-
CZECHOSLOVAK																		
Borovansky & Hnevkovsky[63] (1929)	M	19	17-18	19	14-18	19	18	19	-	-	-	-	-	-	-	-	-	-
ENGLISH																		
Davies & Parsons[62] (1927)	M & F	19-21	16	18-20	15-16	19-20	17	17	19-20	18-19	17	19	19-20	17-18	After 20	18-19	-	-
Paterson[50] (1929)	M	21	19	18-21	18-19	21	19	21	17-18	18	18	18	18-19	18	18	17-18	25	-
	F	18	14	14	14	20	14	20	17	16-17	16-17	16-	16-17	16	15	15-16	25	
Earliest	M	18	18	15	14	17	14	18	17	17	17	17½	17½	15½	17½	15½	22	-
	F	17	12½	13½	12½	18	12½	16	14	14	16	17	15	14	15	14	22	--
Latest	M	21	19	21	19	21	20	21	20	19	18	21	22	19	14	21	28	--
	F	21	17	20	18	20	17	20	20	19	17	21	22	19	24	21	28	--
Difference	M	3	5	6	5	4	6	3	3	2	1	3½	4½	3½	6½	5½	6	--
	F	4	4½	6½	5½	3	5½	4	6	5	1	5	7	5	9	7	6	--

much worn Mixworn other dec. M½ 1

Table No.6.

Ages of Union of Epiphyses as assigned Radiographically in different countries.

Authority Year		Humerus Head.	Humerus Dist.Ex.	Humerus Med.Ep.	Radius Prox.	Radius Dist.	Ulna Prox.	Ulna Dist.	Femur Head.	Femur Ls.Tr.	Femur Gr.Tr.	Femur Dist.Ex.	Tibia Prox.	Tibia Dist.	Fibula Prox.	Fibula Dist.	Clav (st.end)
BURMA																	
Barrett[67] (1936)	F	18	Before 12	14-16	13-16	17-18	12-15	16-18									
EGYPT																	
Sidhom[64] & Derry (1931)	M	-	15-17	18-19	16	18-20	14-20	19-20									
INDIA																	
Basu[45] & Basu (1935-37)	F	15-17	12-13	13-15	13-15	16-18	13-15	16-18	13-15	14-16	13-14	16-18	15-17	14-16	16-18	14-16	
Galstaun[51] (1930-37)	M	14-18	-	16	16	18	17	18	16-17	17	15-17	16-18	16-17	16	14-16	14-16	22
	F	14-16	-	14	14	16½	15	17	14-15	14	15-17	14-15	14-15	14	14-16	13-15	20
Hepworth[65] (1929)	M & F	17-18	14½	-	14-15	16-17	-	16-17	15½-17	16-17	-	16½-17½	16½-17½	16½-17½	16½-17½	17-18	-
Lall[66] & Nat (1934)	M	-	16-19	17-18	16-18	18-19	17	18-19									
Pillai[68] (1936)	M & F	17	-	17	17	18	16	18	15	17	17	17	17	17	17	17	-
Earliest	M	14	14½	16	14	16	14	16	15	16	15	16	16	16	14	14	22
	F	14	12	13	13	16	12	16	13	14	13	14	14	14	14	13	20
Latest	M	18	19	19	18	20	20	20	17	17	17	18	17½	17½	17½	18	22
	F	18	14½	17	17	18	16	18	17	17	17	18	17½	17½	18	18	20
Difference	M	4	4½	3	4	4	6	4	2	1	2	2	½	½	3½	4	nil
	F	4	2½	4	4	2	4	2	4	3	4	4	3½	3½	4	5	nil

much worn Mod. worn
other dec.
M1
1

fusion of certain epiphyses ranges between 1 and 7 years.

This anomaly is due to several factors:-

1). It has been universally accepted since the days of Pryor[57] that epiphyses in girls usually unite about two years earlier than corresponding epiphyses in boys

2). Workers in Burma, Egypt and India (see Table No.6) have shown that, generally speaking, epiphyses fuse about a couple of years earlier in tropical countries than in temperate ones. Galstaun[51] thinks "that the conditions of endocrine balance created by a super-abundance of ultra-violet radiation and warmth tend to produce a condition whereby a greater portion of calcium intake is assimilated and made available for the formation of osseous tissue."

3). The usefulness of the radiological methods in the investigation of epiphysial conditions has been challenged by various observers. Stevenson decries a radiograph as a "confusing medley of shadows". X-ray examination of the intact bone only is subject to the difficulty of interpretation of a picture that contains the super-imposed 'shadows' of the whole thickness of an irregular disc observed from the edge (Glaister & Brash[72]). Sidhom & Derry[64] think that with the radiological method of investigation "error may creep in, since, how far union of an epiphysis with shaft has proceeded is to a large extent dependent on the opinion of the observer in his interpretation of the X-ray film, and this allows of very wide differences in the recorded results. As the cartilaginous interval (between the shaft and its epiphysis) lessens and bony union commences, the extent to which this has happened is often open to question and permits widely differing dates being recorded for the union of epiphysis and shaft". "Even after the epiphysial space has been filled with bone of equal density to the epiphysis and diaphysis (= complete union) and is therefore invisible on the radiogram, a line-like mark sometimes persists into adult life - the so-called 'epiphysial scar'" (Paterson[59]) - which may mislead inexperienced observers into assigning too late a date for epiphysial fusion at any particular area. Flecker[60] interprets this linear shadow as fusion.

Table No.7

Order : PRIMATA Sec : Anthropomorphidae.

Fam or Genus	Homo sapiens (Man).				
Name	------	Black girl (Adelaide).	China-man	Bengali	Malayan
Museum	E.U.A.	E.U.A.	E.U.A.	E.U.A.	E.U.A.
Number	1,VII	68,XVII	68,XV	4,VIII	4,VII
Sex		Fem.	Male	Male	Male
Age	Immature	Young	Adolescent	Adult	Adult
A.EPHIPHYSES					
1.Clav, St.....	x	x	x	x	x
2. Ac.....	x	x	x	x	x
3.Hum, Pr.El..	+	+	+	+	+
4. " & Sh.	-	-	R	R	+
5. Di.El..	+	+	+	+	+
6. " & Sh.	B+	B	+	+	+
7. Lat.Ep.	+	-	+	+	+
8. Med.Ep.	B	-	+	+	+
9.Rad, Prox...	B	-	+	+	+
10. Dist...	-	-	R	R	+
11.Ulna, Prox...	B	-	+	+	+
12. Dist...	-	-	R	R	+
13.Mc, First..	-	-	+	+	+
14. Rest...	-	-	+	+	+
15.Ph(M),Prox...	-	-	+	+	+
16. Mid....	-	- to B	+	+	+
17. Term...	-	B	+	+	+
18.Fem, Head...	-	B	+	+	+
19. Gr.Tr..	-	-	+	+	+
20. Ls.Tr..	-	-	+	+	+
21. Dist...	-	-	R	+	+
22.Tib, Con....	-	-	R	+	+
23. Tb.....	-	-	R	+	+
24. Dist...	-	-	+	+	+
25.Fib, Prox...	-	-	+	+	+
26. Dist...	-	-	+	+	+
27.Calc. Epip...	M	-	+	+	+
28.Mt, First..	M	-	+	+	+
29. Rest...	M	-	+	+	+
30.Ph(P),Prox...	M	-	+	+	+
31. Mid....	M	B to R	+	+	+
32. Term...	M	B to +	+	+	+
33.Ext.Centre...					
B.SPL.FEATURE...					
C.HABITS ETC....					
D.REMARKS.......		Mandible missing			
E.DENTITION.....	Milk	I,C just coming, P1,M1 & 2 in.			

much worn Mworn other dec. M^1

1

> Todd (Todd et al[31]) thinks that owing to the diaphysio-epiphysial union starting deeply and completing on the surface, inspection of the part is apt to give a later date for complete union than that given by X-ray study.
>
> The most reliable method of determining the state of union of an epiphysis is the direct examination of a series of sections of the part of the bone concerned (Glaister & Brash). But differences between the direct and X-ray methods of study may be evaluated and harmonized, at least in man, by constant collateral study in the living and the dead.

The result of radiographic study on epiphyses of 135 Bengalee girls has already been published (Basu & Basu[45]). Besides 35 human skeletons were available for the present study. Table No.7 gives the result of observations on 4 adolescent skeletons from the latter source. The sequence of their epiphysial union is given in Table No.8.

Table No.8

Sequence of Ep. Union in 4 human skeletons
(E.U.A.)

1. Proximal and distal elements and lateral epicondyle of humerus.

2. Terminal phalanges of foot.

3. Distal humeral epiphysis and medial epicondyle with shaft of humerus : Proximal radius : Olecranon ulna : Metacarpals & phalanges of hand : Proximal femur, all : Distal tibia & fibula : Proximal fibula: Calcaneal epiphysis, metatarsals & phalanges of foot.

4. Distal femur : Proximal tibia.

5. Distal radius and ulna : Proximal humerus.

Though sufficient number of skeletons could not be had to discriminate more critically the priority in fusion of the

3 1 3 3 P1 M1 d3 d1 3 2 d3 d&n&3Pm4 M33&1P4 &rupM1-2
much worn Much worn other dec. M^1
1

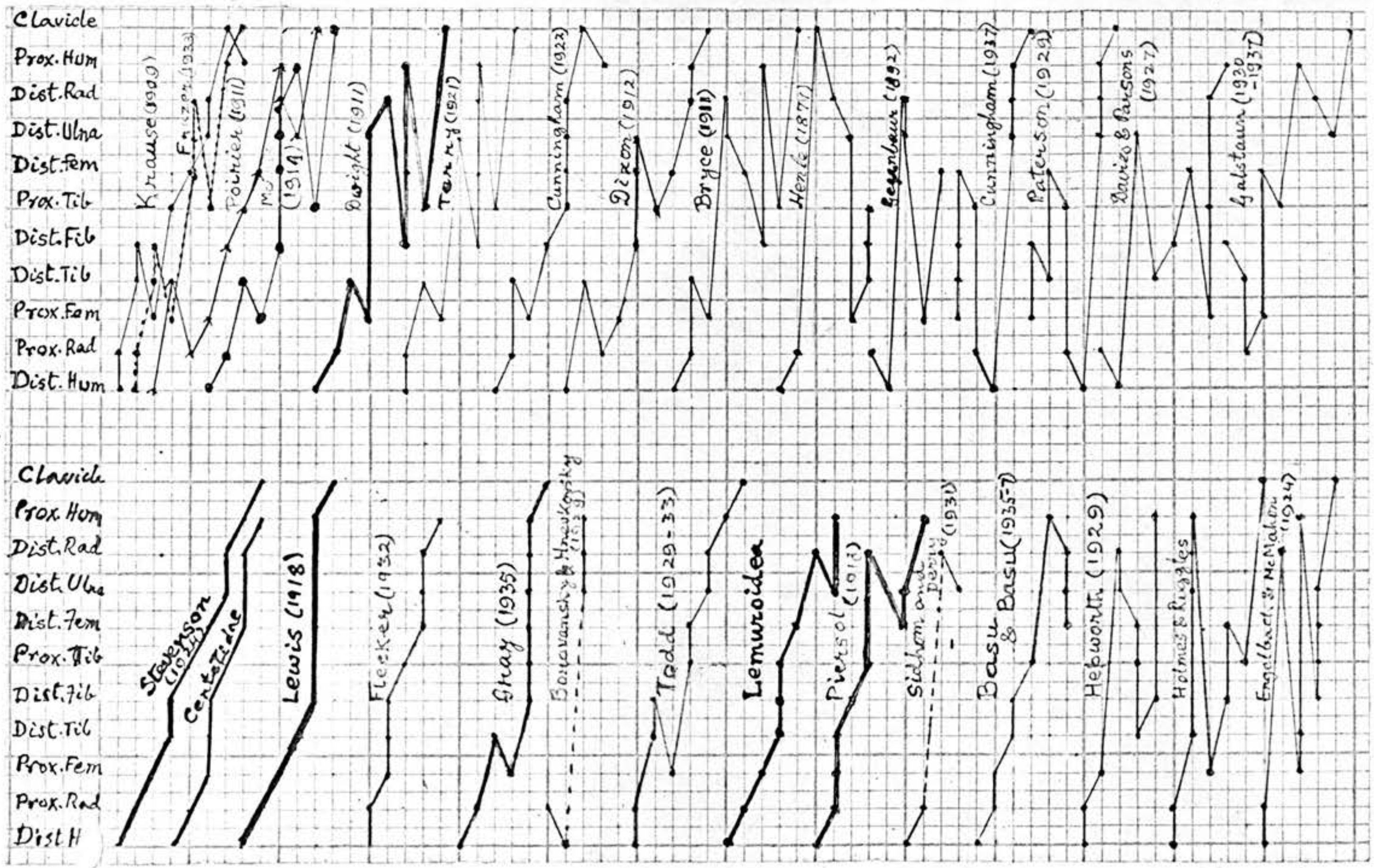


Fig. 9

A graphical representation of the Sequence of Epiphysial Union in limb bones of Man as given by various authors and a comparison of the condition obtaining in other mammals. Stevensoñ's sequence is adopted as the standard for purposes of comparison. Three types of fusion have been described in pp. 240 & 241.

centres in groups 1,3,4 & 5 in the above table, yet on comparison it is found that the sequence revealed in it is substantially the same as that given by Stevenson (Table No.3), except for proximal fibula which, in Table No.8, precedes proximal tibia, and which, according to Stevenson, is inconstant.

Stevenson recognized that the behaviour of certain epiphyses is inconstant and is likely to upset the drawing up of a definite schedule of epiphysial union. These are usually extra-articular, e.g., medial epicondyle humerus, olecranon ulna, femoral trochanters, calcaneal epiphysis, etc. There are others which often have individual variations; proximal fibula, for instance, is more apt to show this feature than proximal tibia. The sternal epiphysis of clavicle is the most 'erratic' member of the family having a long period of epiphysial activity and a late date of fusion (Stevenson). The lateral epiphysis of clavicle, however, is exactly the opposite. It remains distinct for so short a time that it is most often missed as a distinct entity (Todd & D'Errico, Jr.).

In view of the above, Table Nos. 3 & 8 may be looked upon as almost identical. Taking these sequences as representative of man, a graph may be drawn (Fig. 9) with abscissa denoting the epiphyses in the order given by Stevenson and the ordinate showing the sequence in time. The question of exact age is disregarded, since as already

3 1 3 3 P1 M1 a3 a1 3 2 a3 [illegible] M33&1P4 [illegible]
much worn [illegible] worn M1
other dec.
1

indicated there is much disagreement amongst even radiologists about the age at which any particular epiphysis unites and since the other skeletons studied for this work, to which reference may be needed, were mostly collected from wild animals. The sequence given by anatomists (Table No.4) and radiologists (Table Nos. 5 & 6) have been plotted against those in Table No.3. Since Insectivora and Lemuroidea are regarded as the most generalised and primitive of placental mammals (Sedgwick[69], Beddard[70]) the sequence of union of their epiphyses is also represented alongside. It is seen that the sequences as seen in Centetidae (Insectivora) and in Flecker's radiographic work on males agree very closely with Stevenson's results; and those deduced from the works of Basu & Basu (on females), Flecker (on females), Gray, Pillai and Todd as well as the sequence observed in other Insectivora and Lemuroidea do not differ from him very much. Sequences given by Cunningham (1937) and Frazer and those based on radiographic works of Engelbach & McMahon, Hepworth, and Holmes & Ruggles have wider variations. The results of X-ray studies of Davies & Parsons, Galstaun, Paterson and Pillsbury disagree so widely that one almost despairs of any sequence being found from them which may be a common ground for reference of epiphysial studies. Todd's results are the best for various reasons, one being the exhaustiveness and statistical treatment of his data, the other being the constant checking of his results on fresher materials made available through the large opportunities offered by the Brush Foundation of the Western Reserve University.

For skeletal study, therefore, the sequence as given by Stevenson may be taken as standard, or that of Insectivora or Lemuroidea.

The Epiphysial Key: The Todd school favours another method of representing the pattern of epiphysial fusion. On a horizontal base line are represented by three-step vertical lines the modal condition of the series of epiphyses studied in each skeleton. The base line represents the condition of complete non-union ('-'), a height of one step represents beginning union ('B'), that of two steps represents recent union ('R') and complete union ('+') is represented by three steps. The names of the epiphyses are plotted on the base line at unit distances in an order which must be adhered to in all studies. The epiphysial condition will then show various patterns of notches on a series of keys operating the conventional 'barrel & tumbler' locks (Fig. 10).

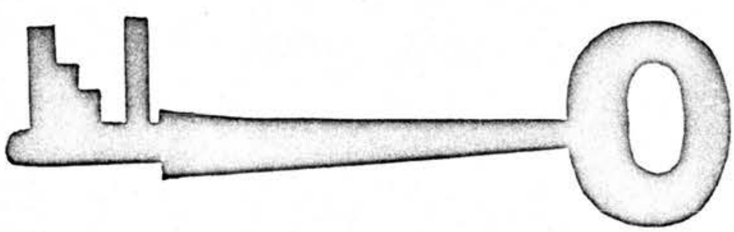


Fig 10

3 1 3 3 P1 M1 d3 d1 3 2 d3 d[illegible] M33&1P4 [illegible]1-2
much worn[illegible]worn M^1
other dec.
1

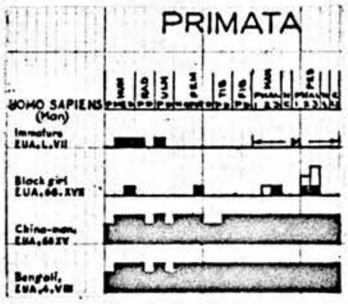


Fig. 11.

Epiphysial chart
for Man.

M stands for a
missing part. Conti-
nuous lines bounding
a clear space indi-
cates precocious epi-
physial activity.

3 1 3 3 P1 M1 d3 d1 3 2 d3 d3n4 M33&1P4 Grup

much worn/Unworn
other dec.

M^1

If such graphs are plotted from above downwards for skeletons showing increasing degree of epiphysial fusion in any group of individuals belonging to a species, genus, family, section or order, it will present the picture of a pattern or 'master key' which will fit in with the epiphysial condition of any member of a similar group and will be comparable to other groups of 'master keys'.

Such a chart is shown in Fig. 11 for the skeletons studied in Table No.7.

The 30 adult human skeletons studied but not represented in the above table are:-

16 in E. U. A. :-	Malayan male (4,VII), Kaffir male(4,LX), Male (1,IV), Male (1,VI), Male (1,VIII), Maori male (69,XXX), Creole (69,XXXI), Eskimo (69,XXXII), Negro A (69,V), Negro B (69,VI), Bushman (68,XIV), Australian (68,XVI), Australian(68,XIX), Andaman Islander, Male (68,XVIII), Man (3,III), Man (3,IV).
1 in E. U. Z. :-	Homo sapiens male (RR,68.2).
2 in R. S. :-	Homo sapiens male (Case 33) : Upper limb of a man compared with those of gibbon, gorilla and chimpanzee (Case 30)
5 in C.M.C.gallery:-	Japanese female, Bengalee female, Bengalee Mahisya male, Nepalese male, Ojibway Salteaux male.
6 in I. M. :-	H. sapiens male (Case 2); Andamanese female (Case 5); Australian female (Case 5); Maori male (Case 4); Bhutia male (Case 4), Upper limb of a man in a comparative series (s.m.g.).

Besides, Prof. Brash very kindly procured for my study the skeleton (not catalogued in E.U.A.) of an eunuch, believed to be about 70 years old, which though fully mature in epiphysis showed 'lapsed union' at crest of ilium, vertebral border of scapula, lapsed and patchy union at sternal epiphysis of clavicle and epiphysial scars at proximal humerus, radius, femur, tibia and fibula and distal radius, ulna, femur, tibia and fibula together with deficiency of compact bone at many of these sites.

3 1 3 3 P1 M1 d3 d1 3 2 d3 d[illegible] M33&1P4 [illegible]
much worn [illegible] worn other dec. $M\frac{1}{}$
1

TABLE NO. 9

List of Insectivora studied.

Family S. Family Genus etc.	Number of Skeletons Total	Young	Adults	bits Spl. features etc.
. Tupaiidae	2	1	1 (WRU ,B211)	Arboreal, diurnal
. Macroscelididae	21	16		Jumping shrews.
Nasilio	19	15	4 (AMNH,86570,F & 86577,F, " 86556,M & 86557,M)	Nocturnal,saltatorial, Metatarsus greatly elongated, tibia and fibula united.
Macroscelides	1	-	1 (WRU, B759)	
Elephantulus	1	-	1 (AMNH, 54013)	
. Erinaceidae	5	5	-	Hedgehogs.
S.F.Gymnuraena			-	Terrestrial, planti-grade, tibia & fibula united.
Hylomys	1	1	-	
Erinaceus	4	4	-	
. Soricidae				Shrews.
S.F. Soricinae				Terretrial, planti-grade.
Neomys	1	1	-	(Neomys is aquatic)
S.F. Crocidurinae				
Crocidura	1	1	-	Terrestrial.
. Talpidae	8	2	6	Moles.
S.F. Talpinae				Terrestrial, planti-grade, strongly fossorial; fore-limbs modified for digging.
Cryptotis	1	3	-	
Scalops	3	-	3 (AMNH, 70283, 100229 & H.L.Hill's, 47)	
Scapanus	1	-	1 (AMNH, H.L.Hill's,48)	
Talpa	3	1	2 (RS,1936, 39.4 and EUA, L23XV)	Powerful burrower
. Potamogalidae	9	8	1 (AMNH,51322)	Otter-like
. Solenodontidae	3	-	3 (AMNH, 35330, 77752, and 77745)	Terrestrial, planti-grade.
. Centetidae	8	6	2	Terrestrial, planti-grade. Ulna & fibula not fused.
Hemicentetes	2	2	-	
Ericulus	2	2	-	
Echinops	2	2	-	
Microgale	2	-	2 (AMNH,31261,F; 31245)	
. Chrysochloridae	4	2	2 (AMNH, mounted spec., WRU, B260)	Golden moles. Burrowers; tibia and fibula united below, 4 fingers & 4 toes.
. Galeopithecidae	2	1	1 (RS, 1932, 64.3)	Volant.

3 1 3 3 P1 M1 d3 d1 3 2 d3 d4nd5M4 M33&1P4 &rupM1-2
much worn M1 unworn
other dec.
M^1
1

Table No. 10

Order: INSECTIVORA Sub-order:

.Fam or enus	Tupai-idae Tupaia	Macroscelididae Nasilio					
ame	F. tana	N. brachy-rhyncha	N. brachy-rhyncha	N. brachy-rhyncha	N. brachy-rhyncha	N. brachy-rhyncha	N. brachy-rhyncha
useum umbor	W.R.U B1363	A.M.N.H 86572	A.M.N.H 86551	A.M.N.H 86566	A.M.N.H 86587	A.M.N.H 86568	A.M.N.H 86575
ex		Female	Male	Female		Female	Female
ge		young	young	young	young	young	adolescent
EPIPHYSES							
Clav, St....	?	B	M	?	x	?	+
Ac....	?	?	M	?	x	?	+
Hum, Pr.El.	+	+	+	+	+	+	+
" & Sh.	B	-	-	-	B	B	B
Di.El.	B	+	+	+	+	+	+
" & Sh.	B	+	+	+	+	+	+
Lat.Ep.	B	+	+	+	+	+	+
Med.Ep.	B	R	+	+	-	+	R
Rad, Prox..	+	+	+	+	+	+	+
Dist..	B	-	-	-	-	B	B-
Ulna, Prox..	+	B	B	B	B	R	+
Dist..	B	F	F	F	F	F	F
Mc, First.	+	B	B	B	B	+	+
Rest..	+	B	B	B	B	+	+
Ph(M), Prox..	+	B	B	B	M	+	+
Mid...	+	B	B	B	M	+	+
Term..	+	+	+	+	M	+	+
Fem, Head..	+	B	B	B	+	+	+
Gr.Tr.	+	-	-	B	B	+	+
Ls.Tr.	+	B	B	B	B	+	+
Dist..	B	-	-	B	B to -	B	B
Tib, Con...	B	-	-	-	B	B	B
Tb....	B	-	-	-	-	B	B
Dist..	B+	B	B	B	B	+	+
Fib, Prox..	B	-	-	-	B	B	B
Dist..	B+	F	F	F	F	F	F
Calc. Epip..	+	B	B	B	-	+	+
Mt, First.	+	B	B	B	B	+	+
Rest..	+	B	B	B	B	+	+
Ph(P), Prox..	+	B	B	B	B	+	+
Mid...	+	B	B	B	B	+	+
Term..	+	+	+	+	+	+	+
Ext.Centre..							

SPL.FEATURE. Radius & ulna, & tibia & fibula are ankylosed

HABITS ETC.. Tree-shrews arboreal; Jumping shrews, saltatorial; metatarsus greatly elongated, specially cuboid & navicular

REMARKS..... Squirrel like; ligamentous sp.

2,1,3,3 / 3 1 3 3 much worn	I1,P1,M1 / P1 M1 M1 worn other dec.	d3,d1,4,2 / d3 d1 3 2	d2,d1,dM2-4 / d3 d[illegible]4 M^1	3,1,4,2 / M33&1P4 erup	M1-2 / M1-2 unworn

Table No. //

Order: INSECTIVORA Sub-order:

.	M a c r o s c e l i d i d a e							
us	N a s i l i o							
s	N. brachy-rhyncha	N. brachy-rhyncha	N. brachy-rhyncha	N. brachy-rhyncha	N. brachy-rhyncha	N. brachy-rhyncha	N. brachy-rhyncha	N. brachy-rhyncha
um	A.M.N.H.	A.M.N.H	A.M.N.H	A.M.N.H.	A.M.N.H.	A.M.N.H	A.M.N.H.	A.M.N.H
er	86553	86583	86591	86558	86563	86554	86565	86560
	Fem.	Fem.	Male	Fem.	Male	Male	Male	Fem.
	adolesc.	adolesc.	adolesc.	adolesc.	adolesc.	adolesc.	adolesc.	adult
	?	+	M	?	+	?	M	+
	?	+	M	?	+	?	M	+
	+	+	+	+	+	+	+	+
	B	B	B+	B+	R	R	+	+
	+	+	+	+	+-	+	+	+
	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+
	B	B-	B	R	R	R	R	+
	+	+	+	+	+	+	+	+
	F	F	F	F	F	F	F	F
	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+
	B	B+	B	B	B	B	R	R
	B	B	B	B	B	R	R	R
	B	B	B	B	B	R	R	R
	+	+	+	+	+	+	+	+
	B	B	B	B	B	R	+	+
	F	F	F	F	F	F	F	F
	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	+	+

Radius is in Nasilio usually longer than humerus

ligamen-tous sp.	ligamen-tous sp.

All standard

THE STUDY OF EPIPHYSIS IN INSECTIVORA.

In page 50A (Table No.9) is shown the number of skeletons, young and adult, studied in the families of this order.

Macroscelididae: Table Nos.10 & 11 show 14 skeletons of Nasilio brachyrhyncha with union of the following epiphyses (for abbreviations see "Abbreviations" at the beginning of this section) :-

1.	In Skel. A.M.N.H,	86572,F,	.. ep. 3,5,6,7,9,17 & 32.
2.	" " "	86551,m,) & 86556,f,)	.. " 8 in addition to above
3.	" " "	86587	.. " 18 in addition to above (15 & 16 missing).
4.	" " "	86568,m,	.. " 13,14,15,16,19,20,24, (26),27 to 31 in addition to above.
5.	" " "	86575,f,) 86553,f,) 86583,f,) 86591,m,) 86558,f,) 86563,m,) 76554,m,)	.. " 11 in addition to above
6.	" " "	86565,m,	.. " 25 & 4 " " "
7.	" " "	86560,f,) 86561,not) tabled.)	.. " 10 in addition to above

8. 4 adult skeletons (Table No.9) show fusion of ep. 21,22 & 23, i.e., those that remain over to unite from the previous stages. They may therefore be considered to be the last to unite in this group.

Table No.12 shows the stages of epiphysial fusion in Macroscelididae, as deduced from the above observations.

Table No. 13

Order: INSECTIVORA Sub-order:

Family or Genus	Erinaceidae				
	Gymnura	Erinaceus			
Name	Hylomys suillus dorsalis	E.europaeus	E.europaeus	E.europaeus	E.europaeus
Museum Number	W.R.U. B 210	E.U.A. L23XV	W.R.U. B 18	E.U.Z. NN 52	R.S. 1935.34
Sex					
Age				young	young
EPIPHYSES					
Clav, St....	-	? (plastered)	B	-	?(wax covered)
Ac....	B	x	B	-	do.
Hum, Pr.El.	+	+	+	+	+
" & Sh.	B	-	B_	-	B
Di.El.	+	+	+	+	+
" & Sh.	+	+	+	+	+
Lat.Ep.	+	+	+	+	+
Med.Ep.	+	+	+	+	+
Rad, Prox..	+	+	+	+	+
Dist..	B	-	-	-	B
Ulna, Prox..	+	B+	R	R	+
Dist..	B	-	-	-	B
Mc, First.					
Rest..	-+	-	B	+	+
Ph(M), Prox..	+	-	B	+	+
Mid...	+	B	+	+	+
Term..	+	B	+	+	+
Fem, Head..	+	+	+	+	+
Gr.Tr.	B	R	+	+	+
Ls.Tr.	B	R	B	+	+
Dist..	B	R	B	+	+
Tib, Con...	B	-	-	-	B
Tb....	B	-	-	-	B
Dist..	B	-	-	-	B
Fib, Prox..	+	-	B	B	+
Dist..	B	-	-	-	B
Calc. Epip..	F	F	F	F	F
Mt, First.	+	B	+	R	+
Rest..	+	-	R to +	+	+
Ph(P), Prox..	+	-	R to +	+	+
Mid...	+	B	+	+	+
Term..	+	B	+	+	+
Ext.Centre..	+	+	+	+	+
SPL.FEATURE.	v.prom. metacromial process	prepollex artic. with radiale			
HABITS ETC..	Terrestrial, plantigrade; radius and ulna free, tibia and fibula fused.				
REMARKS.....					ligamentous sp. readings approx.
DENTITION...	3.1.4.3 / 3 1 4 3 no wear	3.1.3.2 / 2 1 2 3 up. M_3 not in	3.1.3.3 / 2 1 2 3 C like 3rd Incisor	3.1.3.2 / 2 1 2 2 M_3 not in	3.1.3.3 / 2 1 2 2 lower M_3 not in

Table No.12
Stages of Epiphysial Fusion in Macroscelididae.

Stage 1. Proximal elements humerus, terminal phalanges; distal elements humerus; union of latter and lateral epicondyle with shaft humerus: Proximal radius.

Stage 2. Medial epicondyle humerus.

Stage 3. Head femur.

Stage 4. 2nd phalanges, calc. epiphysis, 1st phalanges, metatarsals, metacarpals, femoral trochanters, distal tibia, (distal fibula, fused).

Stage 5. Proximal ulna.

Stage 6. Proximal fibula, proximal humerus.

Stage 7. Distal radius, (distal ulna, fused).

Stage 8. Distal femur and proximal tibia.

In the absence of skeletons of intermediate stages, a more detailed sequence can only be given after referring to the proper stages in specimens belonging to allied genera or families. Distal ulna and fibula, though ankylosed, have been shown in paranthesis to indicate their hypothetical fusion.

Tupaiidae: (Table No.10) Only one specimen of young tupaia was available. It showed union of ep. 3, 9, 11, 13 to 20 and 27 to 32, i.e., upto stage 5 of Macroscelididae, except that distal humeral epiphyses and distal tibia and fibula (5, 6, 7, 8, 24 and 26) were retarded.

Erinaceidae: (Table No.13). 4 skeletons of Erinaceus show the following condition:

1. In skel. E.U.A, LXXXV, union of ep. 3, 5 to 9, 17 & 32, corresponding to stage 2 of Macroscelididae.

2. In skel. W.R.U, B18 additional union of ep. 15, 16, 18, 27 to 31. This shows two intermediate steps of fusion between stages 3 & 4 of Macroscelididae, as may be seen below.

3. In skel. E.U.Z, NN52, further union of ep. 13, 14,19 & 20 provides the next step to reach stage 4 of Macroscelididae.

4. In skel. R.S, 1935.34 the epiphysial condition has overstepped stage 4 of Macroscelididae and got on to its 5th stage; it shows union of ep. 24, (26) & 11.

Only one specimen of Gymnuraena (Hylomys suillus dorsalis, W.R.U, B210) was available. It showed retardation of all proximal femoral epiphyses, others, being in stage 5 of Macroscelididae. Its tail indicates "powers of swimming" (Beddard 70).

The sequence computed from the observations in Macroscelididae and Erinaceidae may be recorded as follows:-

1. Proximal elements humerus; terminal phalanges; distal elements humerus; distal ep. and lateral epicondyle with shaft humerus; proximal radius.

2. Medial epicondyle humerus.

3. Head femur.

4. 2nd & 1st phalanges (manus and pes); calcaneal epiphyses, metatarsals.

5. Metacarpals; trochanters of femur.

6. Distal tibia, (Distal fibula, ankylosed).

7. Proximal ulna.

Up to this, fusion in Macroscelididae and Erinaceidae runs parallel, except occasional retardation of proximal femoral epiphyses, (Hylomys). For want of further evidence the subsequent stages are supposed to be the same as in Macroscelididae, (Stages 6 to 8), or in Centetidae (see pp 55 & 56).

1.incisors

Table No. 14

Order: INSECTIVORA Sub-order:

Soricidae			Talpidae	Chrysochloridae		Gal.eopithecidae
Soricinae	Crociduri-nae		Talpinae			
Neomys	Crocidura	Cryptotis	Talpa	Chrysochloris		Gal.eopithecus
N.fodiens bicolor	C.nyanse kivu	C.parva	T.europea	C.trevelyani	Chrysochloris sp.	G.volans
R.S.	A.M.N.H.	A.M.N.H.	E.U.Z.	W.R.U.	E.U.Z.	E.U.Z.
1937,63	48490	41046	NN 57	B 131	NN 61	NN 65
	Male					
adult	adoloscent	adolescent	adult	young	young	
R	+	x	+	B	nil	nil
?	+	x	+	?	nil	ct.
+	+	+	separate	+	+	+
B ?	R	B	R	-	+	-
+	+	+	+	+	+	+
+	+	+	+	+	+	R
+	+	+	x	+	+	+ ?
+	+	+	x	+	+	+
+	+	+	+	+	+	B
+	R	B	+	-	-	B_
+	+	+	+	B	+ ?	R
+	R	B	+	-	?	nil
+	+	?	+	nil	nil	+
+	+	?	+	+	?	+
+	+	?	+	+	?	+
+	+	?	+	+	?	+
+	+	?	+	+	?	+
+	+	+	?	?	+	B
+	+	+	?	?	+	B
+	+	+	?	?	+	B
+	R	B	+	?	R	B
+	B	B	+	B	+	-
x	B	B	x	B	+	nil
+	+	+	+	B	+	-
+	B	B	+ ?	B	+	-
F	F	F	F	B	+	-
+	+	?	+	+	+	+
+	+	?	+	+	+	+
+	+	?	+	+	+	+
+	+	?	+	+	+	B to R
+	+	?	+	+	+	+
+	+	?	+	+	+	+
rews, terrestrial, rarely aquatic; rat or mouse-ke			clav. & hum. platypus-like	accessory bone growing proximalwards from carpal & parl. to radius & ulna		has patagium, all digits webbed but fingers not elongated
tershrew	terrest.	Fossorial, cursorial or natatorial; fore limbs modif. for digging; short hum. art. with scap & clav.				arboreal, nocturnal insectivorous hang like bat when at rest ed
y minute	tib. & fib. fused			varnished & articulated sp. study ?	ligamentous sp.	ligamentous sp.
x	stand.	stand.	stand.	stand.	stand.	stand.
		no wear				pectinate l.incisors

53a

Table No. 15

Order: INSECTIVORA Sub-order:

Fam or Genus		Potamogalidae Potamogale							
Name		P.velox	P.velox	P.velox	P.velox	P.velox	P.velox	P.velox	P.velox
Museum Number		R.S C,27	A.M.N.H 51327	A.M.N.H 51333	A.M.N.H 51324	A.M.N.H 51317	A.M.N.H 51344	A.M.N.H 51334	W.R.U B212
Sex			Male	Male	Male	Female	Male	Female	
Age		young	young	young	young	young	adolescent	adolescent	young adult
EPIPHYSES									
Clav,	St....	Absent							
	Ac....								
Hum,	Pr.El.	+	+	+	+	+	+	+	+
	" & Sh.	-	-	-	B	B-	B	B	B
	Di.El.	+	+	+	+	+	+	+	+
	" & Sh.	+	+	+	+	+	+	+	+
	Lat.Ep.	+	+	+	+	+	+	+	+
	Med.Ep.	/R	+	+	-	+	+	+	+
Rad,	Prox..	B	B	R	+	+	+	+	+
	Dist..	-	-	-	-	B	B	-	B+
Ulna,	Prox..	B	B	B	B	B	+	+	+
	Dist..	-	-	B-	-	B	B	-	B+
Mc,	First.	B	M	B	R	B	+	+	+
	Rest..	B	M	B	+	B to R	+	+	+
Ph(M),	Prox..	B	M	B	+	+	+	+	+
	Mid...	B	M	B	+	+	+	+	+
	Term..	+	M	+	+	+	+	+	+
Fem,	Head..	B	B	B	B	B+	R	R	+
	Gr.Tr.	B	-	B	B	B+	R	+	+
	Ls.Tr.	B	B	B	B	B+	R	+	+
	Dist..	-	B	-	B	B	B	B to -	R
Tib,	Con...	-	-	-	B	B-	B	R	R
	Tb....	-	-	-	B	B-	B	R	R
	Dist..	B	B	B	R	R	R	+	+
Fib,	Prox..	-	-	-	B	B-	B	B+	B+
	Dist..	B	B	B	R	R	R	+	+
Calc.	Epip..	-B	B	B	+	+	+	+	+
Mt,	First.	B	B	B	R	B	R	+	+
	Rest..	B	B	B	+	B to +	+	+	+
Ph(P),	Prox..	B	B	B	+	+	+	+	+
	Mid...	B	B	+	+	+	+	+	+
	Term..	+	+	+	+	+	+	+	+
Ext.Centre..									
SPL.FEATURE.									
HABITS ETC..		In-habits banks of streams. Has habits of an otter, though insectivorous.							
REMARKS.....		Ligam. sp.				Ligam. sp.			
DENTITION...		M3 not in	M3 crypt. all I not in	up.M3 In. Lower M3 crypt	stand	M3 crypt	stand	stand	stand up.mm still in

Soricidae: (Table No.14). Skel. A.M.N.H, 48490,m, is in stage 5 of Macroscelididae. Skel. R.S, 1937.63, has all epiphyses united except proximal humerus, which may be thought to have changed place with proximal tibia in the sequences given in the foregoing families. Thus it comes fully in line with Stevenson's sequence.

Talpidae: (Table No.14). Skel. A.M.N.H, 41406, is in stage 5 of Macroscelididae. Skel. E.U.Z, NN57, is in a little more advanced stage than that of R.S. 1937.63 of Soricidae, and shows like the latter, that prox. humerus will be the last ep. to fuse.

Potamogalidae: (Table No.15).

1. Skel. R.S, C27, shows union of ep. 3,5,6,7,17 & 32. This represents a further splitting up of stage 1 of Macroscelididae in that proximal radius is separated out and retarded.

2.	Skel.	A.M.N.H,	51327,m,	shows further union of ep.8.
3.	"	"	51333,m,	" " " ep. 31 (acceleration)
4.	"	"	51317,f,	shows further union of ep. 9,15,16, 27, some 29, 30.
5.	"	"	51324,m,	shows further union of ep. 14, 29.
6.	"	"	51344,m,	shows further union of ep. 11 (acceleration), 13.
7.	"	"	51334,f,	shows further union of ep. 19,20, 24,26,28.
8.	"	W.R.U,	B212	shows further union of ep. 18(retardation)
9.	"	A.M.N.H,	51322,m,	is an adult (Table No.9) in which distal radius, ulna and femur and proximal humerus, tibia and fibula are fused.

no weak

other perm. in or cutting

Table No. 16

Order: INSECTIVORA Sub-order:

.Fam or ...nus	Centetidae					
	Hemicentetes		Ericulus		Echinops	
...me	H.madagascarensis	H.madagascarensis	E.telfairi hallescens	E.nigrescens setosus	E.telfairi Martin	E.telfairi Martin
...seum ...mber	W.R.U. B 819	W.R.U. B 130	A.M.N.H. 31270	W.R.U. B 132	W.R.U. B 882	W.R.U. B 133
...x			Female			
...e	y.adult	y.adult	y.adult	y.adult	young	
EPIPHYSES						
Clav, St....	?	A	ot.	A	x	nil
Ac....	-	A	nil	Q	x	nil
Hum, Pr.Ep.	◆	◆	◆	◆	◆	◆
" & Sh.	B	B	B	B	B	B
Di.Ep.	◆	◆	◆	◆	◆	◆
" & Sh.	◆	R	◆	◆	◆	◆
Lat.Ep.	◆	R	◆	◆	◆	◆
Med.Ep.	B	R	B	◆	B	◆
Rad, Prox..	B	B	◆	◆	◆	◆
Dist..	-	B	B	R	B	B
Ulna, Prox..	B	R	B	◆	B	◆
Dist..	B	B	B	R	B	B
Mc, First.	B	◆ ?	B	◆	◆	◆
Rest..	B	B	B	◆	◆	◆
Ph(M), Prox..	B	B	◆	◆	◆	◆
Mid...	◆	◆	◆	◆	◆	◆
Term..	◆	◆	◆	◆	◆	◆
Fem, Head..	B	◆	B	◆	◆	◆
Gr.Tr.	B	R	B	◆	◆	◆
Ls.Tr.	B	◆	R	◆	◆	◆
Dist..	B	B	B	R	B	R
Tib, Con...	B	B	B	◆	B	B
Tb....	B	B	B	◆	B	B
Dist..	B	B	B	◆	◆	B
Fib, Prox..	B	B	B	◆	B	B
Dist..	B	B	B	◆	◆	B
Calc. Epip..	◆	◆	R	◆	◆	◆
Mt, First.	B	◆	B	◆	◆	◆
Rest..	B	B	B	◆	◆	◆
Ph(P), Prox..	B	B	◆	◆	◆	◆
Mid...	◆	◆	◆	◆	◆	◆
Term..	◆	◆	◆	◆	◆	◆
Ext.Centre..						
SPL.FEATURE.	Clavicle curved like a bow					
HABITS ETC..						
REMARKS.....	Ac.end clav. ligamentous; equiv. age in human years is equal to 17				age of eruption of left upper incisor & rt. lower canine	
DENTITION...	lower M_3 not in no wear	standard no wear	standard no wear	standard no wear	dec. can. shedding M_3 not in other perm. in or cutting	upper M_3 not in lower M_3 cut

No sequence in the last mentioned epiphyses can be deduced from skel. A.M.N.H, 51322,m, But skel. W.R.U, B212, shows ep. 10,12,21,22 & 23 in 'R' stage of fusion, therefore they are almost as good as completely fused; ep. 25 is 'B' and ep. 4 is 'B' ; therefore, proximal humerus will most probably be the last to unite, and proximal fibula will immediately precede it. Hence, tentatively the fusion of epiphyses in the next stages may be arranged thus,

10. shows the stage of fusion of ep. 10,12,21,22 & 23.
11. " " " " " " ep. 25, and
12. " " " " " " ep. 4

<u>Solenodontidae:</u> (Table No.9) All adult specimens.

<u>Centetidae:</u> (Table No.16).

1. Skel. W.R.U, B819, shows fusion of ep. 3,5,6,7,16,17,27, 31 & 32, i.e., same as stage 1 of Macroscelididae with proximal radius (9) retarded and calcaneal epiphysis (27) and 2nd phalanges manus and pes (16,31) accelerated. It is also equivalent to stages 1,3 and part of 4 of Potamogalidae.

2. Skel. A.M.N.H, 31270,f, shows fusion of ep. 9, 15 & 30 i.e., head femur is retarded and 1st phalanges are accelerated. It represents part of stage 4 of Macroscelididae and completely agrees with stage 4 of Potamogalidae, barring union of medial epicondyle (8) and some metatarsals (29).

3. Skel. W.R.U, B882 shows fusion of 13,14,18,19,20,24,26, 28,29 and is followed closely by.

4. Skel. W.R.U, B133 showing fusion of ep. 8 & 11. These two last stages represent the same epiphysial condition as in stages 4 & 5 of Macroscelididae.

5. Skel. W.R.U, B132 shows fusion of 22,23 & 25. This may be likened to stage 6 of Macroscelididae in which ep. 4 has been replaced by ep. 22 & 23, a possibility foreshadowed in Soricidae. Since ep. 10, 12 & 21 are in 'R' stage of fusion in this, they may be taken to fuse next. Ep. 4 being in 'B' stage is apparently the last to fuse.

The sequence of epiphysial fusion in Centetidae would therefore be :-

1. Proximal and distal elements humerus; distal elements and and lateral epicondyle with shaft humerus; 2nd and 3rd phalanges; calcaneal epiphysis.

2. Proximal radius, 1st phalanges.

3. Metacarpals and metatarsals, proximal femur (all), distal tibia and fibula.

4. Medial epicondyle humerus, proximal ulna.

5. Proximal tibia and fibula.

6. Distal femur, radius and ulna.

7. Proximal humerus.

The above is in very close agreement with Stevenson's findings.

Chrysochloridae: (Table No.14) Skel. W.R.U, B131, is varnished and not suitable for epiphysial study. Skel. E.U.Z, NN61, is ligamentous and though inconclusive in other respects, shows the following:-

a) Proximal fibula and proximal humerus are fused, when

b) Distal femur is in 'R' stage,

and c) Distal radius and distal ulna (?) in '-' stage.

Therefore these would show the order of epiphysial fusion of the epiphyses bearing the above names.

Galeopithecus: (Table No.14), Skel. E.U.A, NN 65 shows

a) fusion of ep. 3,5,7,8,13 to 17 and 27 to 32, (except some 30
b) fusions of ep. 6 & 11 are in 'R' stage

Hence, it represents stages 1,2 & 4 of Macroscelididae, except proximal radius and femur, and distal tibia and fibula. In other words, the bones of manus and pes have accelerated fusion; distal epiphysis (6) humerus and proximal ulna are slightly retarded. Proximal radius, proximal femur (all), distal tibia and distal fibula are more certainly retarded.

DISCUSSION.

The Influence of Habitat and Mode of Life on Epiphysial Fusion

Reviewing the condition of epiphysial fusion in the families of Insectivora as given in the foregoing account and pending observation to the contrary on more abundant supply of younger skeletal material, one is apt to notice that epiphysial fusion is early modified, though not to a marked degree, by the environments and mode of life of an animal. Thus, Tupaiidae consists of arboreal animals the strength of whose grip on the branches of trees must be early matured; the fusion of epiphyses for the bones of their manus and pes is accelerated in the Macroscelid scale; consequently, the fusion of their epiphyses for distal humerus, distal tibia and distal fibula is relatively retarded. Members of the Galeopithecidae family, again, are adapted for a volant existence. While showing slight retardation of fusion of one of the distal epiphyses (6) of humerus, they exhibit more noticeable retardation in that of proximal radius, and accelerated union of the epiphyses of manus and pes. The epiphyses for proximal femur, distal tibia and distal fibula are relatively retarded in both the above families. Further, Potamogales, having to lead an otter-like existence on muddy and slippery banks of streams must have their grip strengthened. Hence, they have the same sort of accelerations and retardations as stated above, though to a lesser degree.

Macroscelides, on the other hand, are jumping shrews. Their progression is saltatorial, involving considerable strain at elbow, hip and ankle. At the latter situation, the strain is met with in these, as in similar other, animals by (i) the great elongation of metatarsals (compare also Dipodidae, a family of jumping hares, in which metatarsals are elongated; and Galago, Tarsius etc. in which tarsals are elongated), (ii) by the extra rigidity afforded to leg bones by fusion of distal ends of tibia and fibula (compare some rodents and ungulates) and (iii) by the early fusion of distal epiphyses of tibia and fibula, a condition shared by all cursorial terrestrial animals. The epiphyses for distal humerus and proximal radius and femur fused early as a result of this strain. The olecranon epiphysis though erratic (Stevenson) almost keeps pace with the proximal radial.

Erinaceidae, being a family of terrestrial plantigrade animals (except Hylomys, which is partly natatorial), runs parallel to Macroscelididae up to stage 5 of epiphysial fusion of the latter. The available Soricidae and Talpidae skeletons were too few to give any clue to their earlier epiphysial conditions, so that Campbell's[75] theory of aquatic derivation of "true moles" could not be tested against the epiphysial condition in other aquatic Insectivora; yet they showed the same total fusion as stage 5 of Macroscelididae. Centetidae also reaches the same stage after slight retardation in proximal radius and head femur and relative acceleration in others. The available skeletons of Chrysochloridae were too poor in details to indicate stages corresponding to those under review.

<u>The Spurts or Phases of Epiphysial Fusion.</u> Without proceeding further to consider the condition of the remaining epiphyses and looking back over the field covered heretofore, it is seen that the net result of epiphysial activity up to the stage so far studied in available Insectivora skeletons remains strikingly uniform. It seems that in the race for epiphysial fusion, with whatever handicaps from habits or environments the epiphyses might have started and howsoever they speeded up, or slowed down their pace, there comes a stage when fusion is reached by an invariable and constant few of them. The remaining epiphyses, however, will still be active and make a halt only at the next phase of fusion. Epiphysial union in the limbs is thus completed in at least two phases which may be separated by a varying interval of time. Further, during the periods covering these phases, the epiphyses concerned suddenly become conscious of the

approaching fulfilment of their mission and start fusing each at its own speed. This suddenness may very well be likened to a spurt.

The <u>First Spurt or Phase</u> comes at an end when the animal reaches the fifth stage of Macroscelididae, and completes fusion of the following epiphyses:-

(Proximal elements humerus)

Terminal phalanges

(Distal elements humerus)

(Lateral epicondyle humerus): distal epiphysis and shaft humerus

(Medial epicondyle humerus)

Middle phalanges : (calcaneal epiphysis)

Proximal phalanges : proximal radius

Head Femur : (trochanters femur)

Metatarsals

Metacarpals

(Proximal ulna)

Distal tibia : distal fibula.

<u>NOTE:</u> The above order agrees mostly with what obtains in Centetidae, which represents the most generalised type of Insectivora. Extra-articular, erratic and unimportant epiphyses have been placed within parantheses.

It will be seen that the above epiphyses group round the joints of manus, pes, hip, elbow, and ankle. The first spurt of fusion is, therefore, concerned with securing the strength of only one end of the bones entering into the formation of these joints. In other words, one end of each of the main arms entering into the complex lever systems incorporated in the limbs is thereby consolidated.

The Second Spurt or Phase of fusion must necessarily be concerned with the strengthening of the other ends of these arms or levers, namely those that enter into the formation of the shoulder, wrist and knee-joints. Natural conditions do not operate in such a way as to effect simultaneous closure of articular epiphyses at both ends of the chief long bones of a growing animal. The first phase having consolidated one end of the bones at fulcra where the maximum strain is experienced, it remains for the epiphysial cartilages at the other ends to continue their activity undisturbed and add to the lengths of the bones in order that they may adjust themselves, and incidentally the lever systems, to the mathematical needs of the growing dimensions of the body, and to the acquiring of greater skill and force in the execution of its own peculiar movements. The early or late fusion of any of the epiphyses of proximal humerus, tibia and fibula, and distal radius, ulna and femur, will depend on the comparative importance of any of these bones as arms of the lever systems required for skilled movements in the particular habitat of the animals.

> It is worthy of consideration that, epiphysial sequence impressed on the gene, when the animal was in a plastic state, by residence in a particular habitat for millions of years, will not be changed in the major epiphyses if the animal has within a more recent date changed its habitat. It

> will thus be an important piece of evidence in the history or evolution of the animal (compare Campbell[75], who from osteological considerations holds that the terrestrial 'moles' are derived from aquatic ancestors).

In animals with saltatorial habit, an extra length of metatarsals and prolonged growth of femur, tibia and fibula would be an advantage. Hence, it may be expected, that the distal femur and proximal tibia and fibula will, in such animals, be the last to fuse.

> This is found to be true in Macroscelididae with the following sequence of fusion in the second phase:-
>
> Proximal humerus : (proximal fibula)
> Distal radius : (distal ulna, fused)
> Distal femur : (proximal tibia.
>
> It is to be noted that the proximal fibular epiphysis is very often erratic.

The above sequence also shows the relative unimportance of proximal humeral epiphysis in saltatorial animals, so that it fuses early.

> Since Erinaceidae (except Hylomys) shows fusion in the first phase so exactly like Macroscelididae, its second phase of fusion, though not available for the present study, is likely to be similar. One need not be surprised, however, if proximal humerus or distal radius and ulna be the last to fuse in them, as they are not saltatorial. It will then behave as in Centetidae.

Then again, in animals that are strong burrowers, the fossorial adaptation requires that "the limbs should project as little as possible from the sides of the body, while the length of the limbs is retained, and the leverage of the muscles unaffected" (Beddard[70]). The lengthening of the fore-limb is attained by elongation of manubrium sterni carrying with it the clavicles, and transference of the articulation of clavicle from acromion to humerus (Campbell[75]). This is still more aided by the continued growth, till the last, at the proximal end of humerus. Further, the increase in length of humerus is of advantage to other animals who require a large sweep in the movements of their fore-limbs.

This is true of the Moles (Talpidae), of Soricidae and of Potamogalidae. In the former, proximal humerus is the last to fuse. No further details are available in this study. In Potamogalidae, the following is the sequence of union in the second phase:-

Distal radius: distal ulna: distal femur; proximal tibia
(Proximal fibula)
Proximal humerus

The anatomy of the fossorial Chrysochloridae is peculiar. The manubrium and clavicles do not undergo any change. The humerus is lodged in a hollowing out in the walls of the thorax (Beddard); its growth is brought to an end comparatively early. The leverage of the muscles, however, is kept unaffected by the distal radius and ulna growing till the last. The second phase of union in this family, as gathered in this study, is:-

Proximal humerus: proximal tibia: (proximal fibula)
Distal femur
Distal radius, distal ulna (?),

i.e., distal radius and ulna change place with proximal humerus in the sequence in Potamogalidae and probably in Talpidae and Soricidae.

In animals having no special predilection for the habits mentioned above and leading a plain plantigrade terrestrial existence, the sequence in the second phase is the same as that given by Stevenson for Man. This is typically seen in Centetidae and is shown as follows:-

Proximal tibia : (proximal fibula)

Distal femur : distal radius : distal ulna
(any of these may precede the others)

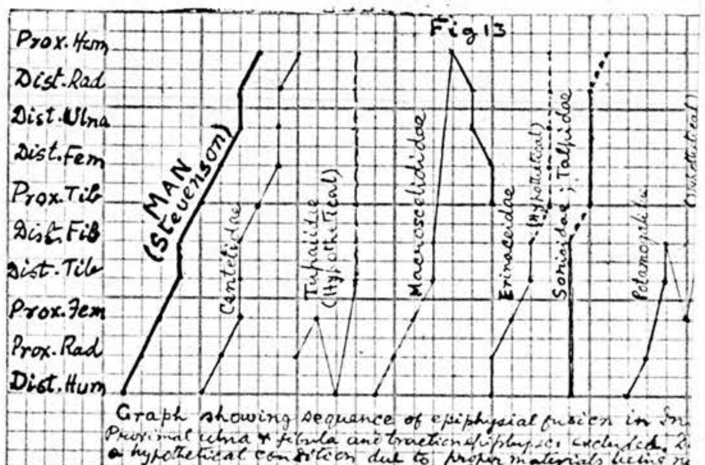
Proximal humerus

In Solenodontidae no young skeleton was available for study and none for the second stage of fusion in Galeopithecidae. The anatomy of Solenodontidae resembles that of Centetidae in many respects.

The above explanations for differences in epiphysial behaviour are, at the best, speculative in view of the paucity of skeletal material in all stages and in all the families of Insectivora. The examination of skeletons of animals of other orders living under similar habitat etc., may show convergence of epiphysial phenomena. The sequence in Centetidae, however, is one that represents a type of fusion characteristic of generalised types of animals which have no special adaptations. But the divergence of sequence of epiphysial fusion in Man as revealed in Table Nos.3,4,5 & 6 and in Fig. 9, cannot but make all optimistic speculations futile, unless more and better co-ordinated work is done in this direction.

Regarding the union of clavicular epiphyses, this work is admittedly defective, often from absent of clavicles and

Fig. 13



Graph showing sequence of epiphysia
Insectivores and Man. Proximal ulna,
fibula, traction epiphyses and those
and pes are excluded. Dotted lines s
thetical condition due to lack of ob
on proper materials.

Abbreviations.:-
F, fusion; M, missing; S.H., study handicapped for various reasons; ?, doubtful reading: hatching of figure indicates that the reading was different in the other limb.

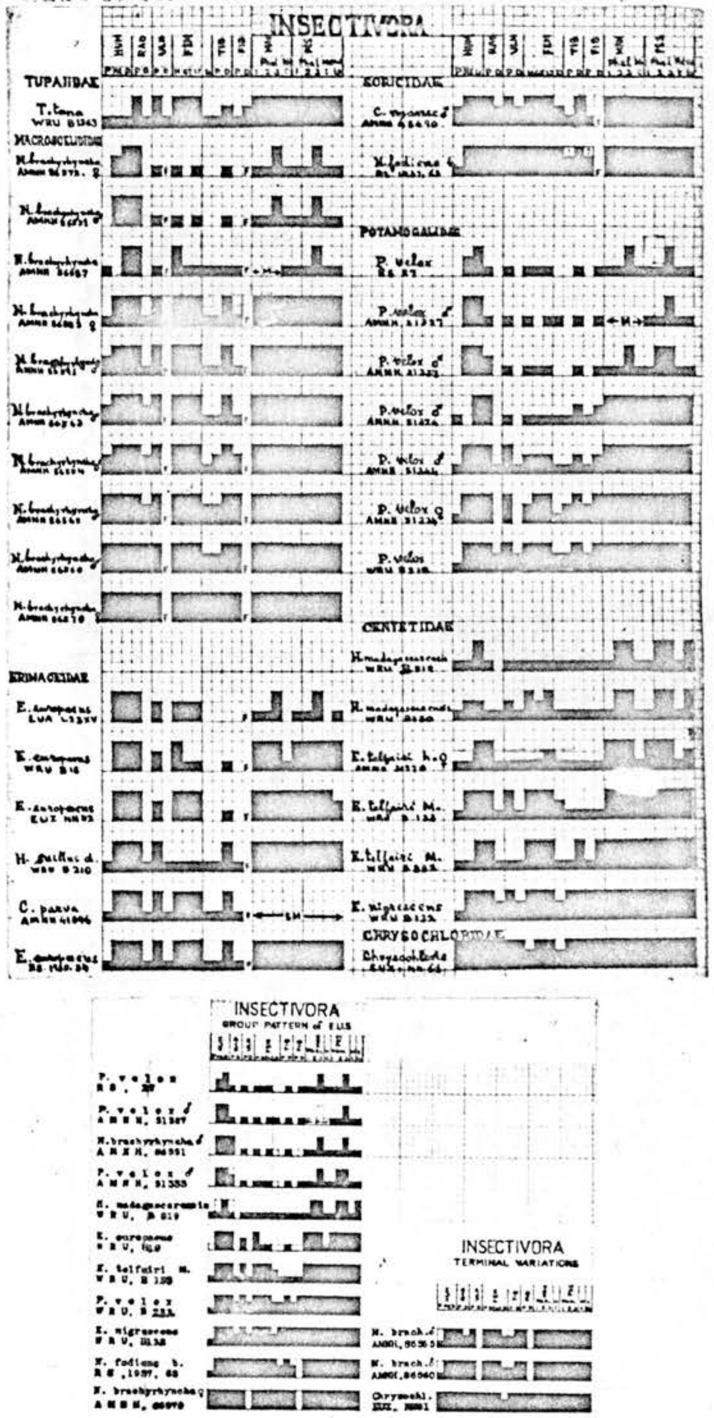


Fig. 12.

Epiphysial Chart for Insectivora.

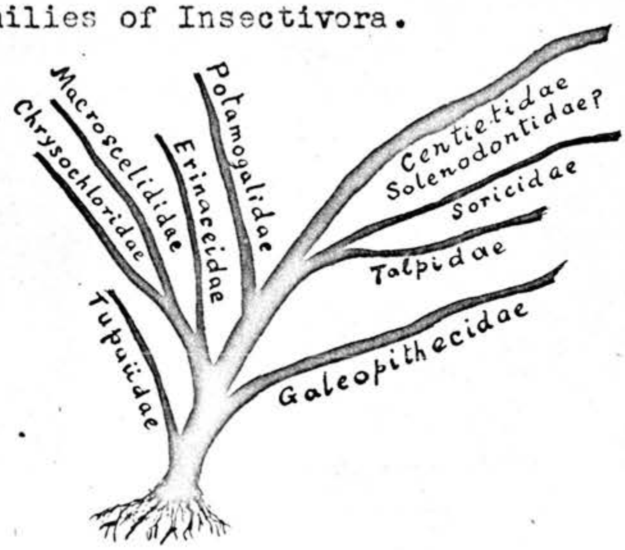
The upper chart represents the sequence in the different families. The lower chart shows the average- or group-pattern of the epiphysunion sequence in the Insectivora and the possible terminal variations. A clear space within dotted lines indicates a hypothetical condition suiting the position.

sometimes from the difficulty of deciding on the stage of union. From the tables, however, it will be seen that they generally fuse much earlier than in Man and within the second stage of epiphysial union. It is sometimes seen that acromial epiphyses have not united when the sternal ones have. This may be a misinterpretation.

The dentition and skull sutures have not been referred to, since occasion for such did not arise.

In the accompanying Epiphysial Charts (Fig. 12) the sequence of epiphysial fusion has been shown in the manner advocated by Todd & Stevenson. 'Terminal variations' indicate the departure in the second phase of fusion from the generalised type represented by Centetidae. The graph (Fig. 13) represents the terminal variations in the different families.

The following diagram (Fig. 14) attempts, tentatively, to show the epiphysial fusion relationships between the different families of Insectivora.



INSECTIVORA
Fig 14.

THE STUDY OF EPIPHYSES IN LEMUROIDEA.

In Table No.17 is shown the number of skeletons studie in the families of this order.

Table No.17

List of Lemuroidea skeletons studied.

Family S.Fam. Genus &c.	Number of skeletons studied. Total	Young	Adult	Habits, Special features
1.Lemuridae	48	16	32	Plantigrade, arbor
S.F.Indrisinae	6	-	6	Hind limbs greatly
Indris	5	-	5 WRU,B343,B1388, B1474,B1475,B1387	developed.
Propithecus	1	-	1 WRU, ----- B1155	
S.F.Lemurinae	18	6	12	Tarsus slightly elongated. Toes n webbed.
Lemur-catta	8	1	7 WRU,B137, B197, B756,B1051,B1157, B1382m,B1383f	Less arboreal than other lemurs.
Other lemurs	6	3	3 WRU,B881, B344, & EUA, 60LV	
Lepidolemur	1	-	1 WRU, ----- B345	
Mixocebus	3	2	1 WRU, ----- B754	
S.F.Galaginae	8	3	5	Calcaneus & navicu elongated.
Galago	6	2	4 WRU,B747,B748;RS, C28; EUZ, RR3	
Microcebus	2	1	1 WRU, ----- B758	Smallest lemur.
S.F.Lorisinae	16	7	9	Sluggish, limbs nearly equal, tars not elongated,hall directed backwards
Perodicticus	6	3	3 WRU, B749, B1039; IM, C13.	
Loris	5	2	3 EUZ, RR4.3; IM,C13; CMC, Gall.	
Nycticebus	5	2	3 WRU, B755; B647; RS,1875, 21.6	
2.Tarsiidae	5	-	5 WRU, B135, B1156, B1229; RS, C28a & C28b.	Arboreal, very lon tarsus, fibula uni with tibia below. P + hallux opposable
3.Chiromyidae	3	2	1 WRU, ----- B198	Squirrel-like. Pollex hallux opposable.
Total	56	18	38	

Table No. 18

Order: PRIMATA Sub-order: Lemuroidea (Prosimii). Fam: Lemuridae

		L.macaco	L.fulves	Mixocebus sp.	L.catta	Lemur sp.	Mixocebus olivaceus	Microcebus murinus	G.alleni
S.Fam or Genus		L e m u r i n a e						G a l a g i n a e	
		Lemur		Mixocebus				Microcebus	Galago
Name		L.macaco	L.fulves	Mixocebus sp.	L.catta	Lemur sp.	Mixocebus olivaceus	Microcebus murinus	G.alleni
Museum		E.U.A.	W.R.U	W.R.U	W.R.U	W.R.U	A.M.N.H	W.R.U	W.R.U
Number		60,V	B1037	B1038	B1029	B138	61589	B434	B757
Sex							Male		
Age			young	y.adult	y.adult				y.adult
A.EPIPHYSES									
1.Clav,	St....	nil	ct.	ct.	ct.	A	+	A	A
2.	Ac....	ct.	ct.	B	ct.	Q	+	B	A
3.Hum,	Pr.Ep.	+	+	+	+	+	+	+	+
4.	" & Sh.	-	B	B-	B	B	R	B	B
5.	Di.Ep.	+	+	+	+	+	+	+	+
6.	" & Sh.	+?	+	B+	+	+	+	+	+
7.	Lat.Ep.	?	+	B	+	+	+	+	+
8.	Md.Ep.	?	B	B	+	+	+	+	+
9.Rad,	Prox..	?	B	B	+	+	+	+	+
10.	Dist..	-	-	B	B	B	B	B	R
11.Ulna,	Prox..	-	B	B	B	+	+	+	+
12.	Dist...	-	-	B	B	B	B	B	B
13.Mc,	First.	?	B	B	+	+	+	+	+
14.	Rest..	?	B	B	+	+	+	+	+
15.Ph(M),	Prox..	?	B	B	+	+	+	+	+
16.	Mid...	?	B	B	B	+	+	+	+
17.	Term..	?	B	B	+	+	+	+	+
18.Fem,	Head..	B?	B	B	B	+	+	+	+
19.	Gr.Tr.	B	B	B	B+	+	+	+	+
20.	Ls.Tr.	ct.	B	B	+	+	+	+	+
21.	Dist..	-	B	B	B	R	R	B	+
22.Tib,	Con...	-	B	B	B	+	R	B	+
23.	Tb....	-	B	B	B	+	R	B	+
24.	Dist..	R	- to B	B	R	+	R	B+	+
25.Fib,	Prox..	-	- to B	B	+	+	R	B	+
26.	Dist..	+.	- to B	B	R	+	R	B+	+
27.Calc.	Epip..	+	B	B	+	+	+	+	+
28.Mt,	First.	?	B	B	+	+	+	+	+
29.	Rest..	?	B	B	+	+	+	+	+
30.Ph(P),	Prox..	?	B	B	+	+	+	+	+
31.	Mid...	?	B	B	+	+	+	+	+
32.	Term..	?	B	B	+	+	+	+	+
33.Ext.Centre..									
B.SPL.FEATURE.									tarsals(calc. & navic.)elongated.
C.HABITS ETC..									
D.REMARKS.....		spec. ligamentous & varnished		lt.scap. ricketty				hum. fractured	calc. = 1/ of tibia navic. much longer than cubgdd.
E.DENTITION...		?	$\frac{1.1.3.3}{2\ 1\ 3\ 3}$		$\frac{2.1.3.2}{2\ 1\ 3\ 3}$	M_3 in not much wear	stand.	stand. no wear	stand. no wear

Lemuridae are arboreal plantigrade animals.

S.F. Indrisinae - No young skeleton was available.

S.F. Lemurinae - 6 young specimens (Table No.18) show fusion of epiphyses in the following order :-

1. In Skel.	W.R.U, B 1038		..	ep.	3,5
2. " "	"	B1037	..	"	6,7
3. " "	"	B1029	..	"	8,9,13 to 17, 20,(25), 27 to 32
4. " "	A.M.N.H,61589,m		..	"	11,18,19,1,2
5. " "	W.R.U, B138		..	"	22,23,24,25,26
6. " "	"	"	presumptively	ep.	21 (in 'R' stage)
7. " "	"	"	"	"	10,12, 4 (in 'B' stage)

(Skeleton E.U.A, 60V has been rejected as it was not suitable for this study).

Hence the sequence of epiphysial fusion in this group is,

1. Proximal and distal elements humerus.
2. Distal elements and lateral epicondyle with shaft humerus.
3. Epiphyses of manus and pes : medial epicondyle humerus : proximal radius : lesser trochanter femur : (proximal fibula); both ends, clavicle.
4. Proximal ulna : head femur : greater trochanter femur.
5. Distal tibia and fibula : proximal tibia and fibula.
6. Distal femur.
7. Distal radius and ulna : proximal humerus.

The above sequence is just the same in the major epiphyses as given by Stevenson, except that proximal fibula may be accelerated. The inconstant behaviour of the latter epiphysis has already been discussed.

Clavicle: acromial epiphysis fuses earlier than sternal. Both are seen fused in skeleton A.M.N.H, 61589 before other centres have completed fusion.

<u>S.F. Galaginae</u> (Table No.18) - 2 young specimens studied. The following order of fusion is seen :-

1. In Skel. W.R.U, B434 .. ep. 3,5,6,7,8,9,11,13 to 20, 27 to 32
2. " " " B757 .. " 21 to 26
3. " " " " presumptively ep. 10 (in 'R' stage) &
4. " " " " " " 12 & 4 (in 'B' stage)

Stage 1 in the above schedule corresponds to stages 1 to 4 of Lemurinae : stage 2 of former with stages 5 & 6 of latter: stages 3 & 4 of former with stages 7 & 8 of latter. Hence the sequence of the last stage of Lemurinae is split up in this family to show, speculatively, that distal ulna or proximal humerus is the last to unite. The sequence in respect of other epiphyses is the same in both the sub-families.(RS,1935,22.8, a juvenile specimen, is rejected).

<u>S.F. Lorisinae</u> (Table No.19) - The animals are nocturnal and sluggish; their tarsals are not elongated. 7 young specimens were studied. In these, the epiphyses were found fused in the

----

mature

Table No. 19

Order : PRIMATA Sub-order : Lemuroidea Fam: Lemuridae

Lorisinae							Chiromyida	
...erodicticus		Loris	Nycticebus					
...potto	P.calabarensis	L.tardigradua	N.borneanus	P.potto	L.tardigradus	N.tardigradus	C.madagascarensis	Chiromyidae sp.
...M.N.H	R.S	A.M.N.H	W.R.U	W.R.U	W.R.U	E.U.Z	R.S.	E.U.Z
...2788	1861,23a	34257	B136	B751	B750	RR2	1889,123.9	RR9.1
...ale	.	Male						
...oung	young		y.adult	y.adult	y.adult		y.adult	
B	x	?	B	A	B	+	x	+
x	x	?	ct.	A	B	+	x	+
+	+	+	+	+	+	+	+	+
-	-	B	B	B	B or -	B	-	+
+	+	+	+	+	+	+	+	+
R	+	+	+	+	+	+	+	+
R	+	+	+	+	+	+	+	+
B	+	+	+	+	+	+	R	+
B	+	+	+	+	+	+	+	+
-	=	-	B	B	B or -	B	-	+
B	+	+	+	+	+	+	+	+
-	-	B	-	B	B or -	B	-	+
B	-	?	M	B	R	+	+	+
B	-	?	M	R	R	+	+	+
B	B	?	M	B	+	+	+	+
B	B	?	M	B	+	+	+	+
R	+	?	M	+	+	+	+	+
B+	B	+	+	?	+	+	?	+
B+	B	+	+	?	+	+	?	+
B+	B	+	+	?	+	+	?	+
B	-	B	B	B	B or -	R	-	+
B	-	B	B	B	B or -	+	-	+
B	-	B	B	B	?	+	-	+
B	B	B	B	B	B+	+	?	+
B	-	B	B	B	B or -	+	-	R
B	B	B	B	B	B+	+	?	+
B	+	B	M	+	+	+	+	+
B	-	?	M	x	R	+	+	+
B	-	?	M	B	R	+	+	+
B	B	?	M	B	+	+	+	+
B	B	?	M	B	+	+	+	+
M	+	?	M	+	+	+	+	+
	v.delicate sp., study approximate	ligamentous sp.		femur ligamentous.		ligamentous sp.	all digits clawed except hallux.	
...and. not ...ally ...ature	stand.	stand.	$\frac{1,1,3,3}{3\ 0\ 3\ 3}$	stand. much worn	stand no wear	$\frac{2,1,2,3}{3\ 0\ 3\ 3}$	$\frac{1,0,1,3}{1\ 0\ 0\ 3}$	$\frac{1,0,1,3}{1\ 0\ 0\ 3}$

following order:-

1. In Skel. A.M.N.H, 52708,m .. ep. 3,5
2. " " R.S, 1861,23a & W.R.U, B751 .. " 6,7,8,9,11,17,27,32
3. " " A.M.N.H, 34257,m & W.R.U, B136 .. " 18,19,20 (manus & pes ligamentous or missing)
4. " " W.R.U, B750 .. " 15,16,30,31
5. " " E.U.Z, RR2 .. " 13,14,22 to 26,28,29
6. " " " " presumptively ep. 21 (in 'R' stage) and
7. " " " " " " 10,12 & 4(in 'B' stage)

From the above it will be seen that the sequence in this sub-family differs from the previous ones by the marked slowing of fusion of its epiphyses in manus and pes.

Tarsiidae. No young skeletons available.

Chiromyidae. (Table No.19) - 2 young specimens studied. The following shows the order of fusion of epiph[illegible]es:-

1. In Skel. R.S, 1889,123.9 .. ep. 3,5,6,7,9,11,13 to 17, 27 to 32 (study of ep. 18,19,20 handicapped)
2. " " E.U.Z, RR9.1 .. The remaining epiphyses fused, except 25 (in 'R' stage)

The total fusion in this family differs from Lemurinae and Galaginae in that the proximal fibula is slightly retarded and is the last to fuse. But, as previously stated on many occasions, this epiphysis is not given much credit as being constant in behaviour.

in.

DISCUSSION.

The total fusion in Lemurinae, Galaginae and Chiromyidae is almost identical with that shown in Centetidae. Lorisinae, however differs considerably in manus and pes. It includes nocturnal animals of very slow movement indicating no great urgency of the bones of manus and pes to fuse in the schedule of fellow lemurs. This is further stressed by the fact that the tarsals in these are not elongated as in their relatives. It seems therefore that the proximal and middle phalanges, metacarpals and metatarsals leisurely run their race for fusion It is curious, however, that the epiphyses for terminal phalanges fuse in scheduled time, probably because digging the terminal phalanges into the surface of soil or branches of trees is essential for animals moving slowly and trying to find their way in darkness or dim light. Calcaneal epiphysis in plantigrade animals is probably equally important; hence this also fuses early in Lorisinae.

The slight variation in Chiromyidae, as seen in proximal fibula, may, in the absence of further evidence be considered as a small individual variation.

The representative sequences in the major epiphyses in Lemuroidea is represented below. The minor and variable epiphyses are put in paranthesis.

(Proximal and distal elements humerus)
Distal epiphysis (and lateral epicondyle) with shaft humerus.
(Terminal phalanges ; Calcaneal epiphysis); proximal radius; (proximal ulna).

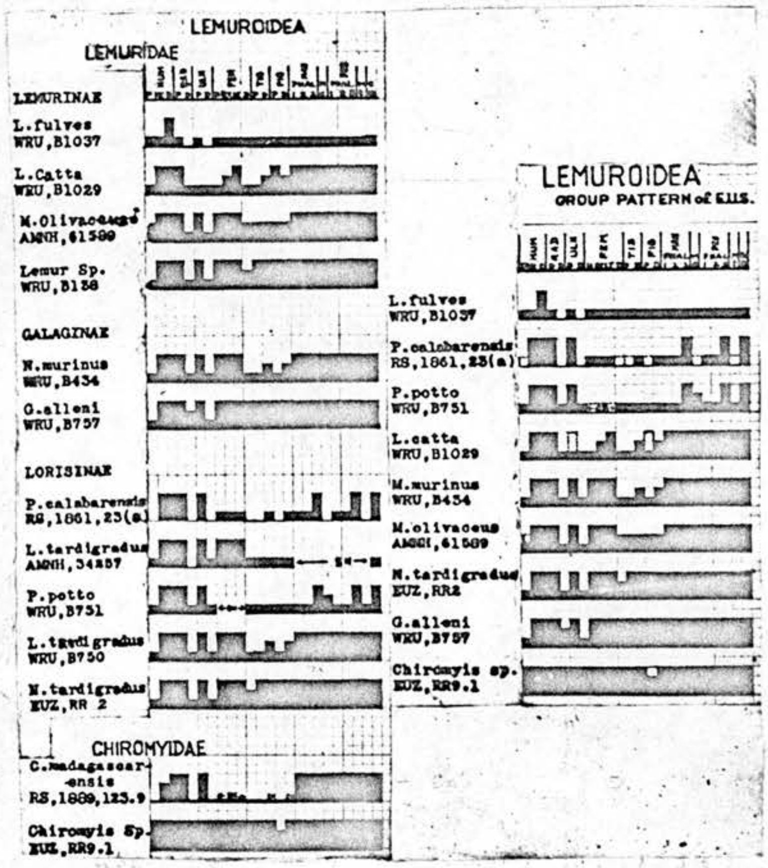


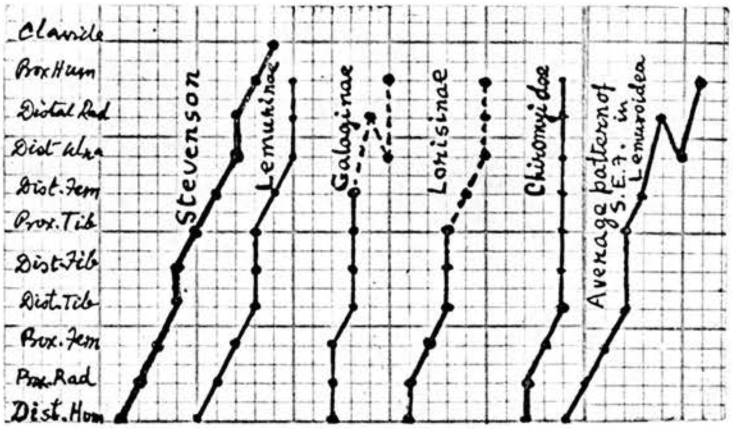
Fig. 11.

Diaphysial Chart for Lemuroidea. On the left [illegible] shown charts of [illegible] Lemuridae and Chiromyidae only. On the right is shown the group [illegible] of [illegible] epiphysial union.

Abbreviations:- [illegible], proximal epiphysis; [illegible], distal epiphysis; [illegible], [illegible] greater and lesser trochanters; [illegible], t, [illegible]; [illegible], metacarpal; cal.ep, calcaneal epiphysis; [illegible], [illegible] various seasons; hatching indicates [illegible] in epiphysial [illegible] in the two limbs; [illegible] lines including a black space [illegible] suppression or [illegible] and continuous lines in similar position, advancement of epiphysial activity.

in.

Fig.16



A graphical representation of S.E.F in different Families of Lemuroidea against Stevenson's schedule. The graph on the extreme right shows the calculated average pattern of S.E.F in this Order. Dotted lines show the trend of union of those epiphyses that were in stages 'R','B',or'-' .

in.

(Medial epicondyle humerus).
Middle and proximal phalanges; metatarsals;
metacarpals..
(Femoral trochanters); head femur.
Distal tibia; distal fibula; proximal tibia;
(proximal fibula).
Distal femur.
Distal radius.
Distal ulna; proximal humerus.

The major epiphyses are thus seen to fuse without differing from Stevenson's schedule. Clavicular epiphyses are uncertain; that at the acromial end fuses earlier than that at the sternal. Both of them were found closed in skeletons A.M.N.H, 61589,m and E.U.Z, RR3, in which all the limb epiphyses were not completely fused.

Epiphysial charts for Lemuroidea are shown in the annexed figures (Fig. 15). Graphs are also shown (Fig. 16) to represent the trend of epiphysial fusion in these animals.

in.

THE STUDY OF EPIPHYSIS IN PRIMATA
other than Man.

Primates are pentadactyle plantigrade mostly arboreal or terrestrial animals. Papio is a rock-dweller.

Sec. 1 PLATYRRHINA or NEW-WORLD MONKEYS.

The tail is prehensile in many of these animals.

In Table No.20 is shown the number of skeletons studied in the families of this section.

Table No.20

List of Platyrrhini studied.

Family S.Family Genus &c.	Number of Skeletons Total	 Young	 Adults	Habits Spl. features etc.
Hapalidae	7	4	3	Arboreal, Fore-limbs shorter than hind.
Midas(Tamarin)	6	3	3 (WRU,B1038, B1035 & B1041)	Pollex not opposable. Tail not prehensile.
Hapale	1	1	-	
Cebidae	25	21	4	Quadrupedal, arboreal.
S.F. Mycetinae	2	2	-	Tail prehensile. Pollex usually well-developed.
Alouata	2	2	-	Pollex & hallux opposable.
S.F. Pithecinae	2	2	-	Tail not prehensile.
S.F. Nycti-pithecinae	8	7	1	Tail not prehensile.
Saimiri	6	5	1 (WRU, B341)	
Callithrix	1	1	-	
Aotus	1	1	-	
S.F. Cebinae	13	10	3	Tail prehensile.
Ateles	5	5	-	Long limbs, pollex reduced.
Cebus	5	4	1 (WRU, B146)	Pollex well-developed.
Lagothrix	3	1	2 (WRU, B876, & B1491)	" " "
Total	32	25	7	

Table No. 21

Order: **PRIMATA** Sub-order: (Sec) Platyrrhina

?.Fam	Hapalidae				Cobidae			
?xx S.Fam.					Mycetinae		Pithecênae	
Genus	Oedipomidas				Alouata		Pithecus	
Name	O.oedipus	O.oedipus	Leontocebus sp.	Hapale sp.	A.seniculus	A.palliata.	P.monacha	P.satanus
Museum	A.M.N.H	A.M.N.H	W.R.U	E.U.Z	R.S.	W.R.U	W.R.U	W.R.U
Number	100007	35910	B1005	RR15.1	1932,64.2	B340	B1489	B1158
Sex			Fem.					
Age							v.young.	

.EPIPHYSES								
.Clav, St....	B	x	ct.	+	x	A	ct.	?
2. Ac....	?	x	B	+	x	A	ct.	?
.Hum, Pr.El.	+	+	+	+	+	+	+	+
. " & Sh.	B	B	B	R	-	B	-	-
. Di.El.	?	+	+	+	+	+	R	+
. " & Sh.	?	+	+	+	+	+	B	B
. Lat.Ep.	?	+	+	+	+	+	-	B
. Med.Ep.	B	+	B+	+	+	+	-	B
.Rad, Prox..	B	R	+	+	+	+	B	B
. Dist..	-	B	B	+	+	B	-	-
.Ulna, Prox..	B	R	+	+	+	+	B	B
. Dist..	-	B	B	+	B	-	B	-
.Mc, First.	B	B	B	+	+	R	B	B
. Rest..	-	B	B	+	+	R	B	B
.Ph(M), Prox...	B	B	B	+	+	+	B	B
. Mid...	B	B	B	+	+	+	B	B
. Term..	B	+	+	+	+	+	B	B
.Fem, Head..	B	+	B	+	+	+	B	B
. Gr.Tr.	B	+	B	+	+	+	B	B
. Ls.Tr.	nil	+	B	+	+	+	nil	B
. Dist..	-	B	B	+	R	+	B	B
.Tib, Con...	-	B	B	+	B	+	B	B
. Tb....	-	B	B	+	B	+	B	B
. Dist..	-	B	B	+	B	+	B	B
.Fib, Prox..	-	B	B	+	B	+	B	B
. Dist..	B	B+	B	+	B	+	B	B
.Calc. Epip..	-	+	B	+	+	x	B	B
.Mt, First.	B	B	B	+	+	M	B	B
. Rest..	-	B	B	+	+	B+	B	B
.Ph(P), Prox..	B	R	B	+	+	+	B	B
. Mid...	B	+	B	+	+	B	B	B
. Term..	B	+	+	+	+	+	B	B
.Ext.Centre..								

.SPL.FEATURE.								
.HABITS ETC..								
.REMARKS.....	ligamentous sp.						patella ossified trochlea not grown well	
.DENTITION...	M_2 in crypt	upper M_2 in crypt	stand.	stand.	stand.	stand.	Lemur stage 148-140. milk dent. M_1 erupting	M_1 just in.

Hapalidae (Table No.21) - Observations of the epiphysial condition in skeletons of 4 young animals reveals fusion in the following order:-

1. In Skel. A.M.N.H, 100007 .. ep. 3, (5,6,7 ligamentous)
2. " " W.R.U, B1005,f .. " 5,6,7,9,11,17,32
3. " " A.M.N.H, 35910 .. " 8,18,19,20,27,31
4. " " " " presumptively ep. 30 (in 'R' stage)
5. " " " " " " 26 (in 'B_+' stage)
6. " " E.U.Z, RR15.1 .. ep. 10,12,13 to 16, 21 to 25,28,29,1,2
7. " " " " presumptively ep. 4 (in 'R' stage)

i.e., (1) Proximal humerus elements.

(2) Distal humerus elements : distal epiphysis and lateral epicondyle with shaft humerus : terminal phalanges : proximal radius : proximal ulna.

(3) Medial epicondyle humerus : proximal femur (all) : calcaneal epiphysis : middle phalanx pes.

(4) Proximal phalanx pes.

(5) Distal fibula.

(6) Distal tibia : metacarpals : proximal and middle phalanges manus : metatarsals : proximal tibia and fibula : distal femur : distal radius & ulna.

(7) Proximal humerus.

This shows that epiphyses of manus and pes except terminal phalanges are all retarded. The main epiphyses, however, though it is difficult to discriminate the priority of their fusion, present the total fusion as similar to that given by Stevenson. Clavicular epiphyses are fused before proximal humeral, in skeleton, EUZ,RR 15.1.

except lower M_3 slight wear | much wear | no wear | no wear | little wear | no wear

Table No. 22

Order: PRIMATA Sub-order: (Sec) Platyrrhina

m.	C e b i d a e						
Fam.	N y c t i p i t h e c i n a e						
nus							
no	S.oerstedi	S.sciurea	S.sciurea	S.sciurea	A.gularis	S.Sciurea	C.jacchus
seum nber	W.R.U. B 1490	W.R.U. B 1034	W.R.U. B 1036	W.R.U. B 1488	W.R.U. B 342	W,R.U. B 826	W.R.U. B 1484
x		Female	Male				
e						y.adult	
	A	-	B	A	A	+	A?
	A	ct.	+?	A	Q?	+	+
	+	+	+	+	+	+	+
	B	B	B	B	B	R	R
	+	+	+	+	+	+	+
	+	+	+	+	+	+	+
	R	+	+	+	+	+	+
	B	B	+	+	+	+	+
	B	+	+	+	+	+	+
	B	B	B	B	B	+	+
	B	+	+	+	+	+	+
	B	B	B	B	B	+	+
	B	B	+	+	R	+	+
	B	B	+	+	B+	+	+
	B	B	+	+	+	+	+
	B	B	+	+	+	+	+
	B	+	+	+	+	+	+
	B	+	+	+	B	+	+
	B	+	+	+	B	+	+
	B	+	+	+	B	+	+
	B	B	B	B	B	+	+
	B	B	B	D	B	+	+
	B	B	B	B	B	+	+
	B	B	+	+	+	+	+
	B	B	B	B	+	+	+
	B	B	+	+	+	+	+
	B	B	+	+	+	+	+
	B	B	+	+	B	+	+
	B	B	+	+	B	+	+
	B	B	+	+	+	+	+
	B	B	+	+	+	+	+
	B	B	+	+	+	+	+
							Lemur stage 70 (about)
	C & M_3 erupting	Stand. except lower M_3 slight wear	Stand. much wear	Stand. no wear	Stand. no wear	Stand. little wear	Stand. no wear

Table No. 23

Order: PRIMATA Sub-order: (Sec) Platyrrhina

			C e b i d a e C e b i n a e				
Cebus	A t e l e s				Lagothrix	C e b u s	
C.capucinus	Ateles	Ateles	A.belzebuth	A.ater	L.lagotricha	C.albifrons	C.unicolor
E.U.A.	E.U.A.	E.U.A.	W.R.U.	W.R.U.	R.S.	W.R.U.	W.R.U.
60,XXXIV	60,XLIX	60,XXXVII	B 141	B 2078	1931,95	B 1159	B 142
		young		Female		Female	y.adult
-	ct.	B	ct.	-	x	x	x
ct.	ct.	ct.	ct.	-	x	x	X
+	+	R	+	+	+	+	+
-	-	-	B	-	-	B	B
+	+	+	+	+	+	?	+
-	R	+	+	+	+	?	+
-	B	ct.	R	+	+	?	+
-	-	ct.	R	B	R	?	R
B	B	B	B	-	- to B	B	+
-	-	-	B	-	-	B	B
B	B	B	B	-	B	B	B
-	-	-	B	-	-	B	B
M	-	B	B	-	-	B	B
-	-	B	- to B	-	-	B	B
-	B	B	- to B	-	B	B	B
B	B	B	B	-	B	B	B
B	B	B	B	-	B	B	B
-	-	B	B	-	B	?	R
-	-	B	B	-	B	?	R
-	-	B	B	-	B	?	R
-	-	-	B-	-	-	B	B
-	-	-	B-	-	-	?	B
ct.	-	ct.	B-	-	-	?	B
-	-	B	B	-	B	?	+
-	-	-	-	-	-	?	B
B	-	B	-	-	B	?	+
-	B	B	B	-	R	B	B
-	-	B	-	-	-	B	B
-	-	B	- to B	-	-	B	B
-	-	B	- to B	-	B	B	R
B	B	B	- to B	-	B	B	R
B	B	B	B	-	B	B	+
	The lt. hum. is a distinct centre			bones fragmented and porotic			
				captive sp. severe case of cage paralysis		sp. unmacerated	
2 crypt	last 3 tooth in each jaw are d.molars	M_3 not in	Stand. much worn		Stand. upper dm_1 just shedding C. erupting	C. erupting M_3 not in	

Cebidae (Table Nos. 21, 22 & 23).

S.F. Mycetinae (Table No.21). 2 specimens were studied. The epiphyses were found to fuse in the following order:-

1. In skel. WRU, B340 .. ep. 3,5 to 9,11,15,16,17, 18 to 21,23 to 26,30,32

2. " " RS, 1932, 64.2 .. " 10,13,14,27,28,29,31 (21 is 'R' & 22 to 26 are B')

3. " " " " presumably ep. 12 (in 'B' stage)

4. " " " " " " 4 (in '-' stage), 1 & 2 (in 'A' stage)

i.e., Proximal and distal elements humerus: distal epiphysis & epicondyles with shaft humerus; proximal radius & ulna: all phalanges (except middle phalanx pes): proximal femur (all): distal tibia & fibula: distal femur; tibia proximal: fibula proximal.

Metacarpals: metatarsals: calcaneal epiphysis: middle phalanx pes: distal radius.

Distal ulna.

Proximal humerus: epiphyses clavicle.

The specimen, (WRU, B340) presents wide divergences in the epiphysial stage of middle phalanx pes, metacarpals and metatarsals (retardation) as compared with the other specimen, which represents a more normal condition. The marked retardation of tibial and fibular epiphyses in specimen, RS,1932,64.2, is explainable by 'lapsed union'. The clavicular epiphyses were active in the above specimens.

S.F. Pithecinae (Table No.21). 2 specimens were obtained for study. The order of fusion is as follows:-

1. In skel. WRU, B1489 .. Proximal elements humerus.

2. " " " B1158 .. Distal elements humerus.

M_3 not in

S.F. Nyctipithecinae (Table No.22) shows 6 skeletons with the following order of fusion :-

1.	In Skel. W.R.U, B1490	..	ep. 3,5,6
2.	" " " B1034,f	..	" 7,9,11,17,18,19,20
3.	" " " B1036,m & B1488	..	" 8,13 to 16, 24,26,27 to 32
4.	" " " B826 & B1484	..	" 10,12, 21 to 25
5.	" " " "		presumptively ep. 4 (in 'R' stage)

Aotus gularis (W.R.U, B349), however, shows a peculiar epiphysial condition ; the epiphysial fusion is intermediate between stages 2 & 3 above, but is retarded in proximal femur (all) and accelerated in proximal fibula. Otherwise the sequence is as follows:-

1. Proximal and distal elements humerus : distal epiphysis and shaft humerus.
2. Lateral epicondyle and shaft humerus : proximal radius and ulna : terminal phalanx manus : proximal femur (all).
3. Medial epicondyle humerus : metacarpals, proximal and middle phalanges, manus : epiphyses, pes : distal tibia and fibula.
4. Proximal tibia and fibula : distal femur : distal radius and ulna.
5. Proximal humerus.

Clavicles: Sternal epiphysis is still active in a Callithrix (W.R.U, B1484) where proximal humerus is 'R', but in a Saimiri (W.R.U, B826) of similar epiphysial age, it has fused.

In this sub-family therefore the major epiphyses have followed Stevenson's sequence.

<u>S.F. Cebinae</u> (Table No.23). Of 10 young skeletons available, Cebus capucinus, W.R.U, B1052, fem., and Ateles ater, W.R.U, B2079, fem., are not shown in the table. The former has been rejected as it was unmacerated. The latter is thrown out since it was in the same stage of fusion as Ateles ater, W.R.U, B2078, fem., both of which were captive animals and showed signs of severe cage paralysis and bony deficiency. Cebus albifrons, W.R.U, B1159, fem., was also unmacerated. The epiphyses in the remaining animals showed the following order of fusion:-

1. In Skel. E.U.A, 60XXXIV & 60XLIX) .. ep. 3,5
2. " " " 60XXXVI & W.R.U, B141) .. " 6
3. " " " B2078 & R.S, 1931.95) .. " 7
4. " " W.R.U, B142 .. " 9,24,26,32
5. " " " " presumptively ep. 8,18,19,20,30 & 31 (in 'R' stage)

Hence the sequence would read as follows:-

Proximal and distal elements humerus.
Distal epiphysis with shaft humerus.
Lateral epicondyle with shaft humerus.
Terminal phalanx pes : proximal radius : distal tibia and fibula.
Medial epicondyle : proximal femur (all) : proximal and middle phalanges pes.

The above result though inconclusive proves, at least, that epiphyses of manus and pes, more particularly of the former

M_3 not in

and of proximal femur are distinctly retarded. Those for distal tibia an fibula are relatively accelerated.

DISCUSSION.

From a reference to Table No.20 it will be seen that many of the New-world monkeys have a prehensile tail. The burden of prehensility on the limbs is thereby reduced. From what has been said in Insectivora, therefore, there will be less urge on the epiphyses of manus or pes or some other epiphyses for union according to the schedule of those not having this special feature. Retardation of such epiphyses may not therefore be out of place. An examination of the findings may bear out the assumption.

Cebidae, for instance, is a family of arboreal animals, many of which have a prehensile tail. In sub-family Mycetinae, Alouata (WRU, B340) shows that though there has been fusion of distal humerus, proximal radius and ulna, and epiphyses at both ends of femur, tibia and fibula, yet those for metacarpals, metatarsals, and some phalanges of the toes are retarded. In Alouata (RS, 1932, 64.2) though retardation has not affected the metacarpals and metatarsals, yet there has been a retardation of tibial and fibular epiphyses, which, if not normal, can only be explained by 'lapsed union'. It must be remembered that fusion of epiphyses for distal tibia, fibula and femur normally precede fusion of that for distal radius in most plantigrade terrestrials. Apart from 'lapsed union', therefore, the condition in specimen RS, 1932,64.2 may be regarded as a retardation arising from loss of urge on union due to imposition of a new condition, namely, prehensility. Sub-family Nyctipithecinae shows six specimens conforming with the first spurt of fusion in Centetidae, except that the proximal and middle phalanges of manus and all the epiphyses of pes are retarded. The early fusion of terminal phalanges of manus, however, is of advantage in long leaps. Aotus gularis, WRU, B349, shows a retardation further of proximal femur (all); acceleration of proximal fibula in this case is not of much value,since this epiphysis is often erratic. This sub-family is not characterized by having prehensile tails. Hence the epiphysial divergence from the generalized type is not marked. Compared with this, members of sub-family Cebinae, characterized by marked prehensility of their tails,show retardation of all the epiphyses of manus and pes and proximal femur, except that terminal phalanges of pes are the first to break the spell of retardation followed closely by the remaining phalanges of pes.

Hapalidae,on the other hand, having no prehensile tail, has normal fusion in its terminal phalanges. Epiphyses of proximal phalanx pes,&proximal & middle phalanges manus only are slightly retarded; that of the head femur is correspondingly accelerated. This arrangement over-comes the non-prehensility of the tail to a certain extent and brings this family partially in line with other families of this order that do not have a prehensile tail, e.g., in Nyctipithecinae, the epiphysial fusion

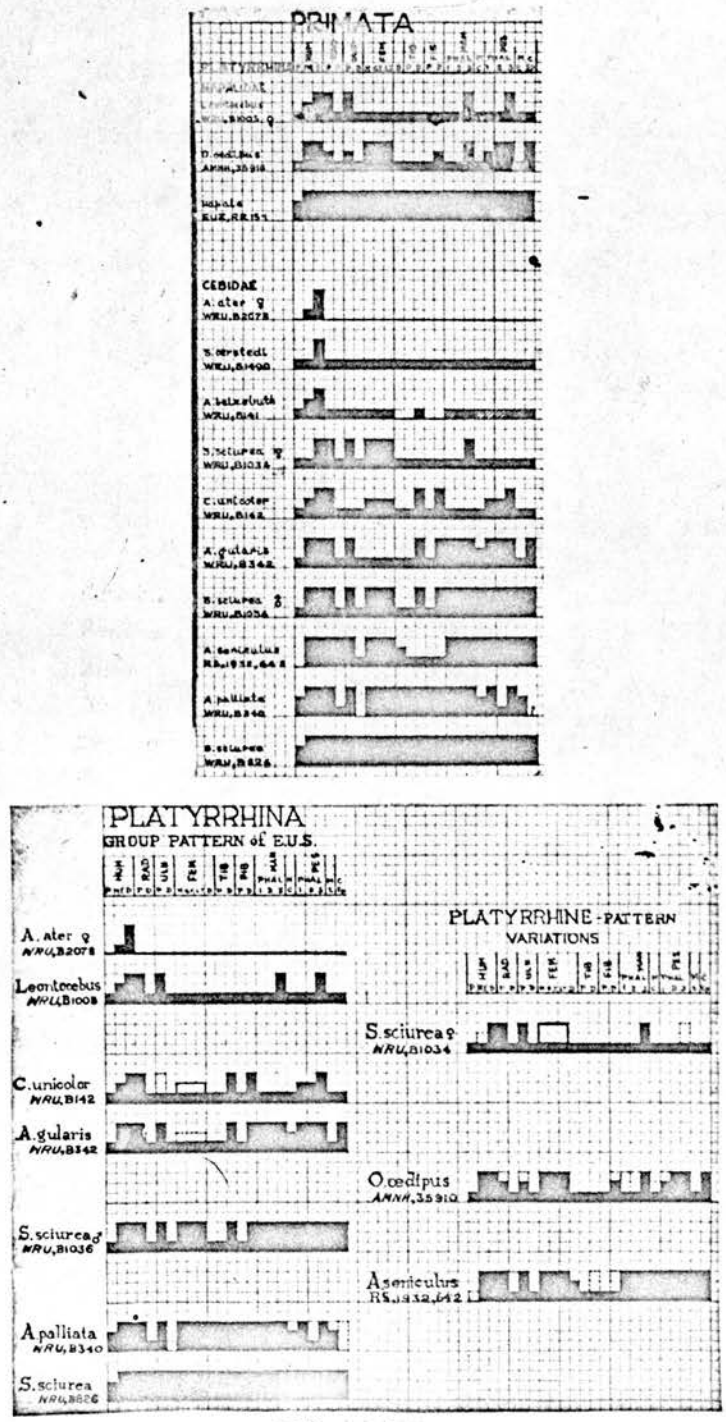


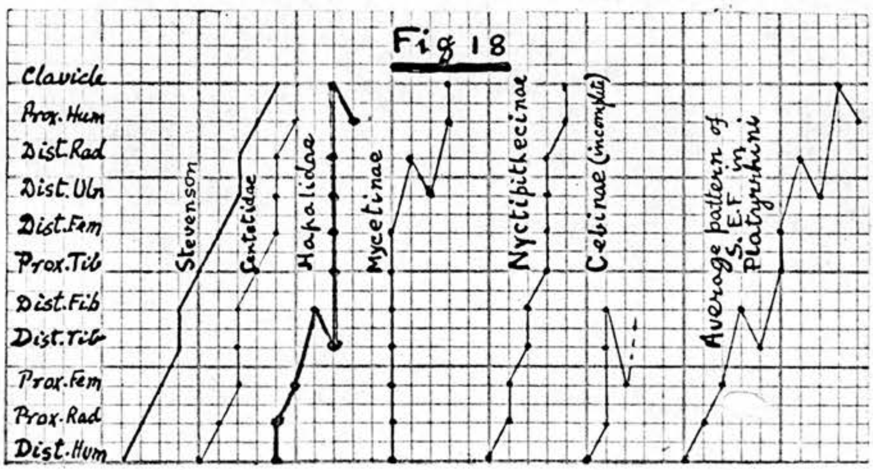
Fig.17..

The Platyrrhine type of Epiphysis Chart.

Above--C.E.F Chart in the differentfamilies.
Below--The group-pattern and pattern variations.
Abbreviations same as in previous charts.
Clear space within full lines means precocious condition.

not mature
M_3 not in

Fig. 18



A graphical representation of the sequence of epiphysial fusion in different families of Platyrrhini against that for Centetidae and the schedule of Stevenson. An average pattern of S.E.F for the group is also given.

resembles that in Hapalidae except that the terminal phalanx of pes also is retarded in the former.

Clavicular epiphyses in both the families complete their fusion earlier than the epiphyses that fuse last in long bones, and, presumably, make the joints at those ends stronger at an early date to bear the strain of long leaps.

From the above consideration, it is seen that retardation of epiphyses of manus and pes and acceleration of proximal femur occur whether or not the tail is prehensile. The prehensility of tail tends to retard the fusion of epiphyses for metacarpals and metatarsals and perhaps of proximal femur and distal ulna; and accelerate those of distal tibia and fibula.

It may be assumed that the original ancestors of the New-world monkeys were all non-prehensile-tailed, like their Old-world relatives, which, as will be seen later, conform to the arboreal modification of the generalized Insectivora type. Retardation in some phalanges of manus and pes and corresponding acceleration of epiphyses at hip and, possibly, at ankle were seen in Hapalidae and Nyctipithecinae as fore-runners of the more pronounced retardations and accelerations that accompanied the permanent attainment of a new feature(namely, prehensility of the tail) in Cebinae and Mycetinae.

Epiphysial charts for Platyrrhines (Fig. 17) and a graph (Fig. 18) of the fusion of their epiphyses as compared with those of Centetidae are attached.

Table No.24

List of Catarrhina skeletons studied.

Family S.Fam. Genus &c.	Number of skeletons studied. Total	Young	Adult	Habits Special features &c.
1. Cercopithecidae	66	42	24	Quadrupedal, hind limbs not much longer than fore. Pollex and hallux opposable. Tail never prehensile.
S.F.Cercopithecinae	52	33	19	Fore & hind limbs sub-equal.
Papio or Cynocephalus (Baboons)	22	12	10 WRU,B151m;B212m; B889f;B890m;B1025m; B1027f;B1028f;B1043m; IM,m.g,C13 & RS,C29	
Cercocebus (Mangabeys)	4	2	2 WRU,B1026f;B1049f	
Cercopithecus or Lasiopyga (Guenons)	9	6	3 WRU,B147m;B1044m; B1032m	
Macacus or Pithecus (Macaques)	16	13	3 WRU,B337m;B1163m; & IM, m.g, C12	
Theropithecus	1	-	1 WRU,B1207m	
S.F.Semnopithecinae	14	9	5 WRU,B1022f;B1050m; B1166m;B1509m; B1510m	Hind limbs longer than fore.
2. Anthropomorphidae or Simiidae	177	63	114	Erect or semi-erect. Tail absent.
Hylobates (Gibbon)	16	7	9 EUA,6OXLVIa; 6OXLVIb;6OXLIV; EUZ,RR45;RS,C30 (comparative); IM, m.g, C2m;WRU, B160m;B161f;B1023	Arboreal. Fore-limbs very long.
Simia or Pongo (Orang Utan)	15	7	8 EUA,6OXLIII;IM, s.m.g; WRU,B172m; B623m;B1168f; B1143f; B1444m	Mainly arboreal. Arms very long; hallux short.
Gorilla	76	27	49 (For list, see text)	More erect & less arboreal than chimp. Fore-arm shorter than arm; heel more developed thumb retrograde; more primitive, but comes nearer to Man in assuming erect posture.
Anthropopithecus (Pan or Chimpanzee)	35	18	17 (For list, see text)	Less erect & more arboreal than gorilla. Fore-arm longer than arm. Thumb not of much use.
Homosapiens	35	4 (see pp.44a & 45)	31 (For list, see pp. 49 & 50)	
	243	105	138	

not mature M_3 not in

Table No. 25

Order: PRIMATA Sub-order: Anthropoidea Sec: Catarrhina

Fam. / S.Fam / Genus	Cercopithecidae / Cercopithecinae / Papio					
P.hamadryas	P.maimon	P.kindae	P.porcarius	P.doguera neuglini	P.doguera toselatus	P.comatus
W.R.U.	E.U.A.	A.M.N.H.	W.R.U.	A.M.N.H.	A.M.N.H.	A.M.N.H.
B 1031	60XLVIII	80796	B 828	52676	51380	80771
Male		Male	Male	Male	Male	
young			young equiv. human age = 18 years			
ct.	-	nil	ct.	M	nil	x
ct.	-	nil	ct.	M	nil	x
+	+	+	+	+	+	+
B	-	B	B	B	B	B
+	+	+	+	+	+	+
+	+	+	+	+	+	+
+	R	+	+	+	+	+
+	R	+	+	+	+	+
B	B	R	R	+	+	+
-	-	B	B	B	B	R
B	B	B+	B+	R	+	+
-	-	B	B	B	- to B	R
B	B	B	B	B	+	+
B	B	B	R	B	+	+
B	B	B	+	B	+	+
B	B	B	+	R	+	+
B	+	M	+	+	+	+
-	B	B	B	R	+	+
B	B	B	R	+	+	+
B	B	B+	+	+	+	+
-	-	B	B	B	B	+
-	-	B	B	B	- to B	+
-	-	B	B	B	- to B	+(L.U)
-	-	B	R	B	+	+
-	-	B-	-	-	B	+
-	-	B	B+	-	R	+
B	+	B	+	R	+	+
- to B	-	B	+	B	+	+
- to B	-	B	+	B	+	+
B	B	B	+	B	+	+
B	B	B	+	R	+	+
B	+	M	+	+	+	+
		ligamentous sp.				
C still in, C erupting M_3 crypt	M_3 not in	up. C shedding lower C not mature M_3 not in	stand. v.sl.wear	2,1,2,3 / 2 1 2 3	stand. C new M_3 unworn	stand. up. C new M_3 unworn

Sec. 2 CATARRHINA or OLD-WORLD MONKEYS.

The tail may be present or absent. When present it is never prehensile.

In Table No.24 is shown the number of skeletons studied in the families of this section.

<u>Cercopithecidae</u>

<u>S.F. Cercopithecinae</u>

<u>Papio</u> shows the following S.E.F. (sequence of epiphysial fusion) in 12 skeletons (Table No.25).

1. In Skel. W.R.U, B1031,m)
& A.M.N.H, 80796,m) .. ep. 3,5,6,7,8
2. " " E.U.A, 60XLVIII .. " 17,27,32 (7,8 in 'R'stage)
3. " " A.M.N.H, 52676,m .. " 9,10,20(27 in 'R' stage)
4. " " W.R.U, B828,m .. " 15,16,28,29,30,31 (9,19 in 'R' stage)
5. " " A.M.N.H, 51380,m .. " 11,13,14,18,24 (26 in 'R' stage)
6. " " " " presumably in ep. 26
7. " " W.R.U, B891,m .. ep. 23,26
8. " " E.U.A, 60XLV .. " 21,22 (23 in 'R' stage)
9, " " A.M.N.H, 80771 .. " 25 (23 L.U)
10. " " W.R.U, B900,m)
& " B892) .. " 10, 1, 2
11. " " " B1503,f .. " 4,12 (21 in 'R' stage)

<u>Cercocebus</u> shows the following S.E.F. in 2 skeletons (Table No.26).

1. In Skel. E.U.A, 60XLVII .. ep. 3
2. " " W.R.U, B752,m .. " 5,6,7

Table No. 26

Order: PRIMATA Sub-Order: Anthropoidea Sec: Catarrhina

C e r c o p i t h e c i d a e

Cercopithecinae

P a p i o (Cynopithecus) C e r c o c e b u s (Cercopithecus)

P.cynocephalus W.R.U B891 male y.adult	C.porcarius E.U.A 60,XLV	P.hamdryas W.R.U B900 male y.adult	P.cynocephalus W.R.U B892 female y.adult	P. hamadryas WRU, B1583?	Cercopithecus sp. E.U.A 60XXXVI young	C.fuliginosus E.U.A 60XLVII young	C.aethiops W.R.U B752 male y.adult	Cercopithecus sp. E.U.Z RR46.2
A	R	+	+	+	ct.	-	-	B
A	R	+	+	+	ct.	x	-	nil
+	+	+	+	+	R	+	+	+
B+	R	B	R	+	-	-	B	B-
+	+	+	+	+	-	B	+	+
+	+	+	+	+	-	B	+	+
+	+	+	+	+	ct.	ct.	+	+
+	+	+	+	+	ct.	-	R	+
+	+	+	+	+	-	B	B	+
-	R	+	+	+	-	-	-	-
+	+	+	+	+	-	-	R	+
B	R	B	R	+	-	-	B	-
+	+	+	+	+	-	B	B	B
+	+	+	+	+	-	B	B	B
+	+	+	+	+	-	B	B	+
+	+	+	+	+	-	B	B	+
+	+	+	+	+	B	B	B	+
+?	+	+	+	+	-	B	-	B
+?	+	+	+	+	-	-	R	+
+?	+	+	+	+	-	-	R	+
R?	+	+	+	R	-	-	-	B
R	+	+	+	+	-	-	-	-
+	R	+	+	+	?	?	-	B
+	+	+	+	+	-	B	B	B
B+	R	+	+	+	-	-	B	B
+	+	+	+	+	-	B	B	B
+	+	+	+	+	ct.	B	B	+
+	+	+	+	+	-	B	B	B
+	+	+	+	+	-	B	B	B
+	+	+	+	+	-	B	B	+
+	+	+	+	+	B	B	B	+
+	+	+	+	+	B	B	B	+
me of un. prox.hum, gamentous		just aft. un.of fem. ep.		SK. at lemur stage between 73 and 61. Osteoarthritis			age in human yrs.= 17	cp. study?
stand. .impacted	stand.	stand. all worn	stand. v.worn		dm still in C.in	dm still in	up.C.crypt lw.C.erupted.	stand.

Table No. 27

Order: PRIMATA Sub-Order: Anthropoidea Soc: Catarrhina

C e r c o p i t h e c i d a e

Cercopithecinae

L a s i o p y g a M a c a c u s (Pithecus)

L.rufoviridis	Lasiopyga sp.	L.pygerythra	L.callitrichus	Pithecus sp.	M.rhosus	Macacus sp.	M.nemestrinus
W.R.U. B 1162 Male	W.R.U. B 1042	W.R.U. B 1021 Male	W.R.U. B 827	W.R.U. B 150 juv.	C.M.C. gal. Male v.young	E.U.A. 60,B v.young	E.U.A. 60,I young
A	x	+	+	M	-	x	ct.
A	x	+	x	M	B	x	ct.
+	+	+	+	-	+	R	R
B	B	R	R	-	-	-	-
+	+	+	+	-	+	B	+
+	+	+	+	-	R	- B	R
+	+	+	+	-	B	nil	ct.
+	+	+	+	-	-	nil	ct.
+	+	+	+	B	B	-	B
B	B	+	B+	-	-	-	-
+	+	+	+	-	B	B	-
B	B	B+	+	-	-	-	-
+	+	+	+	ct.	-	-	-
+	+	+	+	- to B	-	-	-
+	+	+	+	M	-	-	-
+	+	+	+	M	-	-	-
+	+	+	+	M	-	B	B
+	+	+	+	-	-	-	-
+	+	+	+	-	-	-	-
+	+	+	+	-	-	-	-
B	B	+	+	-	-	-	-
B	B+	+	+	- to B	-	-	-
B	B+	+	+	- to B	-	-	-
B+	+	+	+	B	-	-	-
B	B+	+	+	-	-	-	-
B	R	+	+	-	-	-	-
+	+	+	+	-	-	B	B
+	+	+	+	ct.	-	-	-
+	+	+	+	- to B	-	-	-
+	+	+	+	M	-	-	-
+	+	+	+	M	-	-	-
+	+	+	+	M	-	B	B
					ep.8 unites with el. & shaft hum.		supra-sternal bone
			vert.ep. +	ep.loose	zoo spec.		
M_3 in ...rdly worn	C & M_3 er. slight wear	stand. slight wear	stand. much worn some carious	up. M_1 in	up. C & I crypt	up. C in	x

Table No. 28

Order: PRIMATA Sub-Order: Anthropoidea Sec: Catarrhina

C e r c o p i t h e c i d a e									
Cercopithecinae									
M a c a c u s (P i t h e c u s)									Papio
Macacus sp.	M.sinicus	M.rhesus	P.fascicularis	P.albibarbatus	Macacus sp.	Simia Sylvanus	M.rhesus	Cynomolgus fascicul.	P.hamadryas
E.U.A	E.U.Z	W.R.U	W.R.U	W.R.U	E.U.A	W.R.U	RDVC	R.S.	W.R.U
60A	RR43	B460	B1371	B1160	60IV	B1161	B.R.	C.29	B1503
		fem.	male	male		male	fem.		fem.
young	young		young	y.adult			young		y.adult
-	ct.	nil	ct.	ct.	B	A	ct.	x	+
-	ct.	nil	-	ct.	-	A	ct.	x	+
R	+	+	+	+	+	+	+	+	+
-	-	-	-	B-	-	B	B	-	+
B	R	+	+	+	+	+	+	+	+
B	R	+	+	+	+	+	+	+	+
nil	R	R	+	+	+	+	+	+	+
-	B	B	B	R	+	+	+	R	+
B	B	B	R	B	B	+	+	R	+
-	-	-	-	B	-	- to B	B	-	+
B	B	B	B	B	B	+	+	R	+
-	-	-	-	B	-	B	B	-	+
-	-	B	B	B	B	B	-	+	+
-	-	B	B	B	B	B	-	+	+
B	B	B	B	B	B	B	B	+	+
B	B	B	B	B	B	R	B	+	+
B	B	B	B	B	B	+	+	+	+
B	B	B	B	B	B	B	R	+	+
B	B	B	B	B	B	+	R	+	+
B	B	B	B	B	B	B	+	+	+
-	-	-	-	B	B	B	B	-	R
-	B	-	-	B	-	B	B	B	+
-	-	ct.	-	B	-	B	-	B	+
-	B	B	B	B	B	B	B+	B	+
-	-	-	-	B	-	B	-	B	+
-	B	B	B	B	B	B	B+	B	+
B	B	B	B	B	B	+	+	+	+
-	-	B	B	B	B	B	B	+	+
-	-	B	B	B	B	B	-	+	+
B	B	B	B	B	B	B	B	+	+
B	B	B	B	B	B	R	B	+	+
B	B	B	B	B	B	+	+	M	+
creto tres ep.3									lemur stag bet.73 &8]
n ep. ?. well a					ligamentous sp.				osteoarth. hum.& ulna
crypt C crypt	stand.	M_1 stage M2&M3 crypt	M_3 crypt lw.C in	stand. much worn	stand.	stand. much worn	M_3 not in	stand.	stand. much worn

Cercopithecus (Lasiopyga) shows the following S.E.F. in 6 skeletons (Table Nos.26 & 27).

1.	In Skel.	E.U.Z, RR46.2	.. ep.	3,5,6,7,8,9,11,15,16, 17,19,20,27,30,31,32
2.	" "	W.R.U, B1162,m	.. "	13,14,18,28,29
3.	" "	" B1042	.. "	24 (26 in 'R' stage)
4.	" "	" "	presumably ep.	26
5.	" "	" B1021,m	.. ep.	10,21,22,23,25,1,2
6.	" "	" B827	.. "	12 (10 in 'B ' stage)

Macacus shows the following S.E.F. in 13 skeletons (Table Nos. 27 & 28).

1.	In Skel.	E.U.Z, RR43	.. ep.	3, (5 in 'R' stage)
2.	" "	E.U.A, 60I	.. "	5, (3 in 'R' stage)
3.	" "	C.M.C, gal.,m	.. "	3,5
4.	" "	W.R.U, B460,f	.. "	6
5.	" " &	" B1371,m) " B1160,m)	.. "	7
6.	" "	E.U.A, 60XV	.. "	8
7.	" "	W.R.U, B1161,m	.. "	9,11,17,19,27,32
8.	" "	R.D.V.C, B.R,f	.. "	20 (19 in 'R' stage)
9.	" "	R.S, C29	.. "	13,14,15,16,18,28,29, 30,31 (8,9,11 in 'R' stage)

The skeletons in the above genera may be arranged according to the amount of fusion in their epiphyses.

Skel.	E.U.A, 60XLVII	showing fusion of ep. 3
"	E.U.Z, RR43	" " " " 3 (5 in 'R'stage)
"	E.U.A, 60 I	" " " " 5 (3 in 'R' stage)

Skel.	C.M.C, gal.,m	showing fusion of ep.	3,5
"	W.R.U, B460,f	" " " "	3,5 : 6
"	W.R.U, B1371,m) B1160,m) & B 752,m)	" " " "	3,5,6 : 7
"	E.U.A, 60XV) W.R.U,B1031,m) & A.M.N.H,80796,m)	" " " "	3,5,6,7 : 8
"	E.U.A, 60XLVIII	" " " "	3,5 to 8; 17,27,32 (7 & 8 in 'R' stage)
"	W.R.U, B1161,m	" " " "	3,5 to 8,17,27,32 ; 9, 19 & 11
"	A.M.N.H, 52676,m	" " " "	3,5 to 8,17,27,32,9, 19, 20 (27 in 'R' stage)
"	R.D.V.C, B.R,f	" " " "	3,5 to 8,17,27,32, 9,19 : 20 & 11
"	E.U.Z, RR 46.2	" " " "	3,5 to 9,17,19,20, 27,32; 15,16,30,31 & 11
"	W.R.U, B828,m	" " " "	3,5 to 9,15,16,17, 19,20,27,30,31,32; 28,29 (9,19 in 'R' stage)
"	" B1162,m	" " " "	3,5 to 9,15,16,17, 19,20,27 to 32; 13, 14,18
"	R.S, C29	" " " "	same but ep. 8,9,11 in 'R' stage
"	A.M.N.H, 51380,m) & W.R.U, B1042)	" " " "	3,5 to 9,13 to 20, 27 to 32; 24 & 11 (26 in 'R' stage)
"	" "	presumably " " "	3,5 to 9,11,13 to 20,24,27 to 32; 26
"	W.R.U, B891,m	showing " " "	3,5 to 9,11,13 to 20 24,27 to 32;25 & 23

Skel.	E.U.A, 60XLV	showing fusion of ep.	3,5 to 9,11,13 to 20, 24,26 to 32; 22 & 21 (23 in 'R' stage)
"	A.M.N.H, 80771	" " " "	3,5 to 9,11,13 to 24, 26 to 32; 25 (23 L.U)
"	W.R.U,B892; B900,m) & B1021,m)	" " " "	3,5 to 9,11,13 to 32; 10,1 & 2
"	W.R.U, B827	" " " "	1 to 3,5 to 11, 13 to 32; 12 (10 in 'B ' stage)
"	" B1503,f	" " " "	1 to 3,5 to 32; 4 (21 in 'R' stage)

An observation of the above arrangement brings out the following sequence of fusion corresponding to the first spurt in Insectivora :-

Proximal elements humerus
Distal elements humerus
Distal epiphysis and shaft humerus
(Lateral epicondyle humerus)
(Medial epicondyle humerus)
Terminal phalanges, manus and pes : (calcaneal epiphysis)
Proximal radius : (greater trochanter femur : proximal ulna)
(Lesser trochanter femur)
Proximal and middle phalanges, manus and pes
Metatarsals
Metacarpals : head femur
Distal tibia : (proximal ulna)
Distal fibula

In the above analysis it is found that epiphyses 7,8,19, 23 and 27 may be occasionally slightly retarded. These are extra-articular epiphyses and hence, as said before, their fusion value is variable. The olecranon (proximal ulna) epiphysis has a wide range and may fuse at any time between the period of union of proximal radius and that of distal tibia. Proximal radial epiphysis has shown slight retardation ('R' stage) in two specimens only. This is too minute a variation to deserve any notice.

The sequence, shown above, differs from that of the first spurt in Insectivora as seen typically in Centetidae (page 60) in that terminal phalanges are retarded in Cercopithecinae and fuse after distal epiphyses of humerus. The middle and proximal phalanges also are retarded. In other words, all epiphyses at distal end of humerus, and femoral trochanters show relative acceleration in Cercopithecinae; the phalangeal epiphyses are consequently to be regarded as accelerated in Insectivora. The rest of the first spurt of fusion in both the orders is similar. Compared with the sequence in Lemuroidea, there is an acceleration of femoral trochanters only in Cercopithecinae, a fact of no consequence in extra-articular epiphyses. New-World monkeys do not compare favourably in epiphysial fusion sequence with any other group of animals since the prehensility of their tails upsets the first spurt of fusion obtaining in other animals (vide pp 75 to 79).

The epiphyses of proximal tibia and fibula, distal femur, radius and ulna and proximal humerus and clavicular epiphyses (ep. 22,23,25,21,10,12,4,1 & 2), constituting those taking part in the second spurt of fusion in Insectivora, now remain to unite with the shafts. While in six specimens (EUA,60XLV; AMNH,80771; WRU,B892, B900m, B1021m and B827) has distal femur (ep. 21) fused earlier than distal radius and distal ulna (ep. 10 & 12), in only one specimen (WRU, B1503f) it has failed to fuse ('R' stage) when the latter two (ep. 10 &12) and proximal humerus (ep. 4) have fused. Hence the variation is small and individual. In three specimens (WRU, B892, B900m & B1021m) has distal radial epiphysis (ep. 10) fused earlier than distal ulnar (ep. 12) while in one specimen only (WRU, B827) distal ulnar epiphysis has completed fusion when distal radial is almost in 'R' stage ('B '); hence the latter may also be taken as a case of individual variation. The only remaining epiphysis to fuse is the proximal humerus (ep. 4) which, but for the specimen WRU, B1503,f out of eight specimens, would unquestionably be the last. For the same reason as advanced in the case of distal femur the variation is small and negligible.

Clavicular epiphyses (ep. 1 & 2) are found to have fused along with distal radius and onwards. They are accelerated, as compared to the schedule of Man, in the same way as in Insectivora, Lemuroidea and Platyrrhina.

The sequence of fusion in Cercopithecinae in the stage corresponding to the second spurt of fusion in Centetidae (Insectivora) may, therefore, be indicated as follows:-

(Tubercle of tibia)
Proximal tibia
Distal femur

(Proximal fibula)
Distal radius : acromial and sternal epiphysis of
clavicle
Distal ulna
Proximal humerus

The only difference in the above series is that proximal fibula fuses after distal femur whereas in Centetidae and Lemuroidae it fuses before the latter. This is a small variation in view of the inconstancy of the proximal fibular epiphysis, as mentioned before.

Table No. 29

Order: PRIMATA Sub-Order: Anthropoidea Sec: Catarrhina

C e r c o p i t h e c i d a e

Semnopithecinae

S e m n o p i t h e c u s (P y g a t h r i x)

Semnopithecus E.U.A. 60VI juv.	Semnopithecus E.U.A. 60VII young	P.pileata W.R.U. B1165 young	P.entellus W.R.U B153 y.adult female	Colobus vellerosus R.S. 1861.52.1A	P.entellus W.R.U. B1511 y.adult female	P.cristata W.R.U. B1164 y.adult female	S.entellus E.U.A. 60III	P.rubicunda W.R.U. B622 adult female
ct.	B	ct.	A	x	A	?	R	A
ct.	B	+?	A	x	A	?	-?	A
B	+	+	+	+	+	+	+	+
-	B	B	B	B	B	B	B	R
B	+	+	+	+	+	+	+	+
-	+	+	+	+	+	+	+	+
-	+	+	+	+	+	+	+	+
-	+	+	R	+	+	+	+	+
-	+	+	+	+	+	+	+	+
-	-	B	B	-	B	+	R	+
-	R	+	+	+	+	+	+	+
-	B	B	B	-	B	+	R	+
-	B	B	B	rud	B	+	+	+
-	B	B	B	+	B	+	+	+
-	B	B	+	+	B	+	+	+
-	B	B	+	+	B	+	+	+
-	B	B	+	+	R	+	+	+
-	B	B	R	+	+	+	+	+
-	B	B	R	+	+	+	+	+
-	B	B	+	+	+	+	+	+
-	-	-	-	B	B	B	R	+
-	-	B	-	B	B	B+	+	+
ct.	-	B	-	R	B	B+	+	+
-	B	B+	R	+	B	+	+	+
-	-	B	-	B	- to B	+	R	+
?	B	B	B	+	B	+	+	+
-?	+	+	+	+	R	+	+	+
-	B	B	B+	+	B	+	+	+
-	B	B	B+*	+	B	+	+	+
-	+	B	+	+	B	+	+	+
-	+	B	+	+	B	+	+	+
-?	+	B	+	+	R	+	+	+
			*ep.mtV = +		styloid ulna art. with ulnare & pisiform			
ocid. ent.	stand.	dc & dm still in M_3 crypt	stand.	stand.	stand. no wear	stand. moderate wear	stand.	period of suture closure stand. moderate wear

S.F. Semnopithecinae

The following S.E.F. is seen in 9 young skeletons (Table No.29).

1. In Skel. W.R.U, B1165 .. ep. 3,5,6,7,8,9,11,27
2. " " E.U.A, 60VII .. " 30,31,32 (11 in 'R' stage)
3. " " W.R.U, B158 .. " 15,16,17,20(8 in 'R'stage)
4. " " " B1511 .. " 18,19 (17,27 & 32 in 'R' stage & ep. 15,16,30,31 in 'B' stage)
5. " " R.S, 1861,52.1a .. " 13,14,24,26,28,29
6. " " E.U.A, 60III .. " 22,23 (10,12,25 in 'R' stage)
7. " " W.R.U, B1164 .. " 10,12,25
8. " " " B622 .. " 21 (4 in 'R' stage)
9, " " " " presumably ep. 4

i.e., Proximal and distal elements humerus : distal epiphysis (and lateral and medial epicondyles) with shaft humerus : proximal radius (proximal ulna : calcaneal epiphysis)

All phalanges pes

All phalanges manus : (lesser trochanter femur)

Head femur : (greater trochanter femur)

Metacarpals : metatarsals : distal tibia : distal fibula : proximal tibia

Proximal fibula : distal radius : distal ulna

Distal femur

Proximal humerus

The clavicular epiphyses in this series are still active where the limb epiphyses have fused. They are thus a closer approach to Stevenson's schedule. The other epiphyses as compared to Cercopithecinae show a retardation of epiphyses for manus and pes, distal femur and a relative acceleration of proximal radial and proximal femoral epiphyses in Semnopithecinae.

Table No. 30

Order: PRIMATA Sub-order: Anthropoidea Sec: Catarrhini

m	A n t h r o p o m o r p h i d a e.					
s	Hylobates or Gibbon					
	H.hoolock	Gibbon	H.hoolock	H.agilis	H.concolor H.	H.agilis
um	I.M	E.U.Z	W.R.U	R.S	W.R.U	W.R.U
er	M.g: C.8	RR37-1	B159	1902.35.D4	B162	B1048
	male		male	male	female	male
	young	young	y.adult	young	young-	young
IPHYSES						
av, St....	-	ct.	ct.	x	A	A
Ac....	ct.	ct.	ct.	x	-	A
n, Pr.El.	+	+	+	+	+	+
" & Sh.	-	-	-	B	B	B
Di.El.	+	+	+	+	B	+
" & Sh.	+	+	+	+	B+	+
Lat.Ep.	+	+	R	+	B	+
Med.Ep.	R	B	R	B	B	+
, Prox..	-	B	B	B	B	+
Dist..	-	-	-	-	B	B
a, Prox..	R	B	R	R	B	+
Dist..	-	-	-	-	B	B
First.	-	B	B to -	-	B	B+
Rest..	-	B	B to -	-	B	B+
M),Prox..	-	B	B to -	- to B	B	B+
Mid...	-	B	B to -	B	B	+
Term..	-	B	B	B	B	+
, Head..	-	-	-	B	B	+
Gr.Tr.	-	-	B	B	B	+
Ls.Tr.	nil	nil	ct.	B	B	+
Dist..	-	-	-	-	B	B+
, Con...	-	-	-	-	B	B+
Tb....	-	-	-	-	B or nil	B+
Dist..	-	-	-	-	B	R
, Prox..	-	-	-	-	B	R
Dist..	-	-	-	-	B	R
c. Epip..	+	B	B	B	B	+
First.	-	-	B to -	-	B	B+
Rest..	-	-	B to -	-	B	B+
P),Prox..	-	-	B	B	B	B+
Mid...	-	-	B	B	B	+
Term..	-	-	B	B	B	+
.Centre..						
.FEATURE.						
ITS ETC..						
ARKS.....	art.skel. ep.loose		art.skel.			art.skel.
	up.C erupting Lw.C just in, M3 crypt	dc's still in, P's just in, M3 not in	M3 not in	M3 erupting.	many d still in, M1 only in	up.M3 erupting, lw. 3 crypt

Anthropomorphidae.

More or less arboreal. Tailless. Erect or semi-erect. In the former case progression is entirely on hind limbs, in the latter tips of fingers or knuckles may be used to assist in locomotion. Pollex is always and hallux usually opposable.

Genus Hylobates. (Gibbons)

Smallest and most freely tree-frequenting in the whole family. Fore-limbs very long but not used to assist hind limbs in walking. Flat of sole is fully on the ground when the animal walks.

6 young skeletons were available (Table No.30). Besides, there was a very juvenile skeleton (EUA, 60L) which was rejected from this study. The S.E.F. is noted below:-

1.	In Skel.	W.R.U, B162,f	..	ep.	3
2.	" "	" B159,m	..	"	5,6
3.	" "	E.U.Z, RR37.1 & R.S, 1902,35.14,m	..	"	7
4.	" "	I.M, m.g, C8,m	..	"	27
5.	" "	W.R.U, B1048,m	..	"	8,9,11,16 to 20,31, 32

i.e., Proximal elements humerus

Distal elements humerus : distal epiphysis with shaft humerus

(Lateral epicondyle humerus)

(Calcaneal epiphysis)

(Medial epicondyle humerus) : proximal radius : proximal ulna : middle and terminal phalanges, manus and pes : proximal femur, all

The rest were all open.

This represents the same picture as in the corresponding epiphyses of Cercopithecinae or Semnopithecinae, except that in Hylobates the proximal phalanges, metatarsals, metacarpals are slightly retarded, thereby relatively accelerating the epiphysis for head femur.

Table No.31

Order: PRIMATA Sub-order: Anthropoidea Sec: Catarrhini

Fam.		A n t	h r o	p	o i	d e	a
Genus				P o n g o (Simia or Orang)			
Name		Pongo pygmaeus	Pongo	P.pygmaeus	Pongo sp.	Orang	P.pygmaeus
Museum		W.R.U	W.R.U	W.R.U	R.S	I.M	W.R.U
Number		B1024	B1169	B625	C,31	m.g,C2	B1444
Sex						female	male
Age		juv.	juv.	juv.		y.adult	adult
A.EPIPHYSES							
1.Clav,	St.....	ct.	ct.	-	x	A	+
2.	Ac.....	ct.	nil	ct.	x	+	+
3.Hum,	Pr.El..	+	+	+	+	+	+
4.	" & Sh.	-	-	-	-	+	+
5.	Di.El..	-	-	B	+	+	+
6.	" & Sh.	-	B	B	+	+	+
7.	Lat.Ep.	ct.	-	B	+	+	+
8.	Med.Ep.	ct.	-	B*	+	+	+
9.Rad,	Prox...	B	B	B	+	+	+
10.	Dist...	-	-	-	-	R	+
11.Ulna,	Prox...	ct.	-	B	+	+	+
12.	Dist...	-	-	-	-	R	+
13.Mc,	First..	- to B-	B	B-	B	+	+
14.	Rest...	- to B-	B-	B	- to B	+	+
15.Ph(M),	Prox...	- to B-	B-	B	- to B	+	+
16.	Mid....	- to B-	B	B	- to B	+	+
17.	Term...	- to B-	B	B	R	+	+
18.Fem,	Head...	B	-	-	+	+	+
19.	Gr.Tr..	B	-	-	+	+	+
20.	Ls.Tr..	B	-	-	+	+	+
21.	Dist...	-	-	-	B	+	+
22.Tib,	Con....	-	-	-	B	+	+
23.	Tb.....	x	ct.	-	B	+	+
24.	Dist...	-	-	-	B	+	+
25.Fib,	Prox...	-	-	-	B	+	+
26.	Dist...	-	-	-	-	+	+
27.Calc.	Epip...	- to B-	ct.	B	+	+	+
28.Mt,	First..	- to B-	B	B to -	B	+	+
29.	Rest...	- to B-	B-	B	B	+	+
30.Ph(P),	Prox...	- to B-	B-	B	B	+	+
31.	Mid....	- to B-	B-	B	B	+	+
32.	Term...	- to B-	B	B	+	+	+
33.Ext.Centre...							
B.SPL.FEATURE..		all embedded in ct.		*ep.8 unites with troch. & shaft hum.		os centrale present in wrist	
C.HABITS ETC...							
D.REMARKS......				ep. loose		artic.skel.	
E.DENTITION....		all deciduous	M2 stage M3 crypt	lw.P1&2 in lw.C erupting	stand.	stand.	stand.

Genus Simia or Pongo. (Orang-Utan).

Body massive. Fore-limbs reach upto ankle. Pollex and hallux small. They walk on the outside of their feet with knuckles on the ground. No ligt. teres on head femur.

5 young skeletons are shown listed in Table No.31. The fore-limbs of another were studied in a comparative series in the Small Mammal Gallery of the Indian Museum. In this specimen ep. 1,2,4,7 to 16 were completely open; ep. 6 & 17 were in 'B' stage and ep. 3 & 5 were closed.

There were two very juvenile skeletons (WRU, B1397 & B1442,m). Most of their epiphyses being still in cartilage, the specimens were rejected from this study. Specimen WRU, B1024, though in a similar stage, has been kept to give an idea of the epiphysial condition of the rejected specimens which were still younger.

The S.E.F. stands as follows:-

1.	In Skel.		W.R.U, B1169 & B625	..	ep.	3
2.	"	"	I.M, s.m.g, comp.	..	"	5
3.	"	"	R.S, C31	..	"	6,7,8,9,11,18,19,20, 27,32
4.	"	"	I.M, m.g, C2	..	"	4,13 to 17, 21 to 26 28 to 31
5.	"	"	W.R.U, B1444,m	..	"	10 & 12

i.e., Proximal elements humerus
Distal elements humerus
Distal epiphysis and condyles with shaft humerus : proximal radius : proximal ulna : proximal femur, all : calcaneal epiphysis : terminal phalanges pes

Terminal phalanges manus : proximal and middle phalanges manus and pes : metatarsals and metacarpals : distal tibia and distal fibula : distal femur : proximal tibia, fibula and humerus : acromial epiphysis clavicle.

Distal radius : distal ulna : sternal epiphysis clavicle

The above shows the marked retardation of epiphyses of manus and pes and relative acceleration of proximal radius, ulna and femur. Proximal humerus, however, fuses early along with distal femur leaving distal radius and distal ulna to fuse last of all the long bone epiphyses. This reminds one of the various possibilities in Man as shown in Table Nos.4, 5 & 6.

<u>Genus Gorilla.</u> Semi-erect animals, more terrestrial than arboreal. Most of them dwell in plains (Gorilla gorilla Wymann), some live in mountains (Gorilla berenei). They are a nearer approach to Man than the previous genera (Hylobates and Simia). Their bodies are massive; fore-limbs reach to middle of leg; hallux well-developed ; heel better developed than in Simia; and they can stand and walk without assistance of their arms, though usually they walk with backs of their hands on the ground and on the flat of their soles.

Krogman divides the eruption of teeth in gorilla into six stages. The physical growth of the animals may be correlated to these dental periods or ages. The following shows the dental formulae for the different ages:-

<u>Stages of tooth erruption in Gorilla (Dental age)</u>

Stage I $\frac{i\ 1,2}{i\ 1,2}$, $\frac{c}{c}$, $\frac{m\ 1,2}{m\ 1,2}$

" II $\frac{i\ 1,2}{i\ 1,2}$, $\frac{c}{c}$, $\frac{m\ 1,2}{m\ 1,2}$, $\frac{M\ 1}{M\ 1}$

" III $\frac{I\ 1,2}{I\ 1,2}$, $\frac{c}{c}$, $\frac{Pm\ 1,2}{Pm\ 1,2}$, $\frac{M\ 1}{M\ 1}$, $\frac{M\ 2\ er}{M\ 2\ er}$

" IV $\frac{I\ 1,2}{I\ 1,2}$, $\frac{C\ er}{C\ er}$, $\frac{Pm\ 1,2}{Pm\ 1,2}$, $\frac{M\ 1,2}{M\ 1,2}$, $\frac{M\ 3\ er}{M\ 3\ er}$

" V $\frac{I\ 1,2}{I\ 1,2}$, $\frac{C\ new}{C\ new}$, $\frac{Pm\ 1,2}{Pm\ 1,2}$, $\frac{M\ 1,2,3\ (new)}{M\ 1,2,3\ (new)}$

" VI $\frac{I\ 1,2}{I\ 1,2}$, $\frac{C}{C}$, $\frac{Pm\ 1,2}{Pm\ 1,2}$, $\frac{M\ 1,2,3}{M\ 1,2,3}$, all worn.

Two skeletons in dental age I were availed in WRU. These were B169,m and B1858,m (wet preparation). Both showed that the epiphyses were mostly in cartilage. They were rejected from this study.

Five skeletons of stage II were studied in WRU. All of them were wet preparation. Specimens B1424,f ; B1760,m and B1929,f have not been shown in Table No. 32, as they did not show anything more than specimens B1931,m and B1933,m. Specimen B1424,f showed the proximal humeral elements fused when none else had fused.

Five specimens in dental age III were availed in WRU. Specimen B1783,f was a dry preparation, the rest were all wet. It along with specimens B1844,m and B,1935,m has been listed in Table No.32. Specimens B1753,f and B1850 have not been included in the table, as they did not provide much material for study.

Six specimens of dental age IV were studied in WRU (Table Nos. 32 & 33). Except B 1781,m, all were wet preparations.

Of dental age V, WRU provided 14 specimens, 7 of which (including 2 wet specimens along with a solitary specimen from AMNH (No.90194) are included in Table Nos.33 & 34. The remaining ones had completed fusion of epiphysis of long bones of limb. They were, WRU, B1416,m ; B1746,m ; B1710,f ; B1787,m ; B1754,m ; B1717,m and B1846,f.

Dental age VI was found in 42 skeletons studied:-

A. 41 skeletons of Gorilla g.Wymann were obtained as follows -

(i) 36 specimens in WRU with complete epiphysial fusion, viz, B624,m ; B1411,m ; B1712,m ; B1756,f ; B1728,m ; B1765,f ; B1797,m ; B1798,f ; B1057,m ; B1409,m ; B1704,f ; B1430,m ; B1417,m ; B1731,m ; B1431,m ; B1733,m ; B1752,f ; B1730,m ; B1407,m ; B1852,f ; B2745,m ; B1796,m ; B1806,f ;B1851,f ; B2741,m ; B1725,f ; B1849,f ; B1729,m ; B1408,m ; B1736,m ; B3543,m ; B3547,m ; B3548,m ; B3556,m ; B3557,m ; B3558,m ; B3546,m,

(ii) 2 specimens in IM ; the one, a female specimen in Mammal Gallery, Case 2 showing all epiphyses united (see Table No.34), except distal radius ('R' stage) and distal ulna ('B?' stage) ; the other, a male specimen in Mammal Gallery, Case 2, was fully matured in all limb ep.,

(iii) 2 specimens in RS, one showing the fore-limb only in a comparative series in Case 30 (all ep. closed), the other in Case 32 was also fully adult, and

(iv) 1 specimen, 64XXX, in EUA. It was an old adult.

Table No. 32

Order: PRIMATA Sub-order: Anthropoidea Sec: Catarrhini

L.Fam or Genus	A n t h r o p o m o r p h i d a e					
	G o r i l l a					
Name	G.gorilla Wymann	G.gorilla Wymann	G.gorilla Wymann	G.gorilla Wymann	G.gorilla Wymann	G.gorilla Wymann
Museum	W.R.U.	W.R.U.	W.R.U.	W.R.U.	W.R.U.	W.R.U.
Number	B 1933	B 1931	B 1783	B 1844	B 1935	B 1860
Sex	Male	Male	Female	Male	Male	Male
Age	young	young	young	young	young	y.adult
A.EPIPHYSES						
1.Clav, St....	ct.	ct.	-	ct.	ct.	ct.
2. Ac....	ct.	ct.	-	ct.	ct.	x
3.Hum, Pr.El.	+	+	+	+	+	+
4. " & Sh.	-	-	-	-	-	-
5. Di.El.	+ ?	+	-	-	B	+
6. " & Sh.	-	-	-	-	B	B
7. Lat.Ep.	ct.	ct.	-	ct.	B	-
8. Med.Ep.	-	-	-	-	B	B
9.Rad, Prox..	-	-	-	-	B	-
10. Dist..	-	-	-	-	-	-
11.Ulna, Prox..	ct.	ct.	ct.	ct.	B	ct.
12. Dist..	-	-	-	-	-	-
13.Mc, First.	B	-	-	B	-	-
14. Rest..	B	-	-	B	-	-
15.Ph(M), Prox..	-	-	-	B	-	-
16. Mid...	-	-	-	B	-	-
17. Term..	-	-	B	B	-	M
18.Fem, Head..	-	-	-	-	-	-
19. Gr.Tr.	-	-	-	-	B	-
20. Ls.Tr.	ct.	- to B	-	ct.	- to B	+
21. Dist..	-	-	-	-	- to B	-
22.Tib, Con..	-	-	-	-	B	-
23. Tb....	-	-	-	-	ct.	ct.
24. Dist..	-	-	-	-	B	B
25.Fib, Prox..	-	-	-	-	-	-
26. Dist..	-	-	-	-	-	B
27.Calc. Epip..	-	-	-	B	B	B
28.Mt, First.	-	-	-	B	B	-
29. Rest..	-	-	-	B	B	-
30.Ph(P), Prox..	-	-	-	B	B	-
31. Mid...	-	-	-	B	B	-
32. Term..	-	-	B	B	B	M
33.Ext.Centre..						
B.SPL.FEATURE.	ep.8 cont. with troch. & sh.hum.	ep.8 cont. with troch. & sh.hum.			ep.8 cont. with troch. & sh.hum.	
C.HABITS ETC..		Plains Gorilla				
D.REMARKS.....	wet prep.	wet prep.	dry sp. ep.loose ct.shrunk	wet prep.	wet prep.	wet prep.
E.DENTITION...	M_1 in no wear Dental age II	M_1 in some wear Dent.age II	M_2 up. in do. lw.cr. Dent.age III	M_2 up. & lw. crypt Dent.age III	M_2 in Dent.age III	M_3 crypt Dent.age IV

Table No. 33

Order: PRIMATA Sub-order: Anthropoidea Sec: Catarrhini

A n t h r o p o m o r p h i d a e

G o r i l l a

	G.gorilla Wymann	G.gorilla Wymann	G.gorilla Wymann	G.gorilla Wymann	G.gorilla Wymann	G.gorilla Wymann	G.gorilla Wymann	G.gorilla Wymann
m	W.R.U.	W.R.U.	W.R.U.	W.R.U.	W.R.U.	W.R.U.	A.M.N.H.	W.R.U.
r	B 1932	B 1751	B 1761	B 1928	B 1780	B 1930	90194	B 274
	Female	Male	Male	Female	Male	Male	Female ?	Female
	y.adult	y.adult	y.adult	y.adult	y.adult	y.adult	y.adult	y.adult
	ct.	ct.	A	ct.	ct. ?	ct.	?	A
	ct.	x	A	ct.	x	ct.	nil	+
	+	+	+	+	M	+	+	+
	B_	B	-	- to B	-	B	-	-
	+	R	+	+	+	+	+	+
	R	R	B	+	+	+	+	+
	R	B	B	R	+	B	+	+
	B +	- to B	B	R	+	R	+	+
	- to B	-	-	-	M	-	+	+
	-	-	-	-	M	-	-	-
	-	B	B	R	M	B	+	+
	-	-	-	-	M	-	B	-
	M	B	-	-	M	-	M	B+
	M	B	-	B	M	-	M	B+
	M	B	-	-	M	-	M	+
	M	B	-	-	M	-	M	+
	M	R	M	B	M	- to B	M	+
	-	R	-	R	+	-	+	+
	B	-	-	B	+	B	+	+
	R	B	-	+	+	B	+	+
	-	-	-	B+	B	B	-	-
	-	-	-	B	-	B	B	- to B
	-	-	-	-	?	ct.	B	B_
	-	B	-	B	B_	B	B+	B
	-	-	-	-	M	B	-	-
	- to B	-	-	-	M	-	B	B
	M	R	B	B	M	B	M	+
	M	B	-	B	M	-	M	+
	M	B	-	B	M	-	M	R to +
	M	B	M	-	M	-	M	R
	M	B	M	-	M	-	M	+
	M	B	M	-	M	-	M	+
	ep. 8 cont. with troch. & sh. hum.		ep. 8 cont. with troch. & sh. hum.					
	P l a i n s			G o r i l l a				
	wet prep.	wet prep.	abt.14 human yrs.	wet prep.	wet prep. fragment.	wet prep. ep.= D.age IV		
	Dental age IV	Dent.age IV	Dent.age IV	Dent.age IV	Dent.age IV	Dent.age V	Dent.age V	Dent.age V

Table No. 34

Order: PRIMATA Sub-order: Anthropoidea Sec: Catarrhini

.	Anthropomorphidae						
ns	Gorilla						
.	G.gorilla Wymann	G.gorilla Wymann	G.gorilla Wymann	G.gorilla Wymann	G.gorilla Wymann	G.gorilla Wymann	G.berinei
eum ber	W.R.U. B 1425	W.R.U. B 1764	W.R.U. B 1709	W.R.U. B 1953	W.R.U. B 2739	I.M. M.g.C.2	F.M. 26505
	Male y.adult	Female y.adult	Male y.adult	Female y.adult	Male adult	Female y.adult	 adult
	A	A	A	x	A	+	+
	A	A	?	x	+?		+
	+	+	+	+	+	+	+
	B	-	B	B	R	+	+
	+	+	+	+	+	+	+
	+	+	+	+	+	+	+
	+	+	+	+	+	+	+
	R	+	+	+	+	+	+
	B	+	+	+	+	+	+
	-	-	B	B+	+	R	+
	+	+	+	+	+	+	+
	-	-	B	B+	R	B?	+
	B	+	+	+	+	+	+
	B	B+ to R	+	+	+	+	+
	B	+	+	+	+	+	+
	+	+	+	+	+	+	+
	M	+	+	+	+	+	+
	B	+	+	B	+	+	+
	B	+	+	R	+	+	+
	- to B	+	+	R	+	+	+
	B	B	B+	B	+	+	+
	B	B	+	B+	+	+	+
	B	B	+	+	+	+	+
	- to B	B	+	R	+	+	+
	B	- to B	B+	R	+	+	+
	B	B	+	+	+	+	+
	B	+	+	+	+	+	+
	B	R	+	+	+	+	+
	B	B+ to +	+	+	+	+	+
	B	+	+	+	+	+	+
	B	+	+	+	+	+	+
	M	+	+	+	+	+	+
	Plains Gorilla						Mountain Gorilla
	sk. at Lemur stage 122 = 16 human years		abt.24 human years	wet prep.			
	Dental age V	Dent.age V	Dent.age V	Dent.age V	Dent.age V	Dent.age VI	Dent.age VI

B. Only 1 skeleton of G. beringei was availed in the Field Museum (No.36505); it was fully adult (Table No.34).

The epiphyses that were found fused in the specimens described above and in Table Nos. 32, 33 & 34 are shown below, arranged according to the stages of their dental age.

Dental Age I. Epiphyses mostly in cartilage; all open.

Dental Age II.

In skel.	WRU,	B1760m,		fusion	of	ep.	nil
"	"	"	B1424f;B1929f; B1933m	"	"	"	3
"	"	"	B1931m	"	"	"	3,5

Dental Age III.

In skel.	WRU,	B1753f;B1783f; B1844m;B1935m		"	"	"	3
"	"	"	B1850m	"	"	"	3,5

Dental Age IV.

In skel.	WRU,	B1751m		"	"	"	3
"	"	"	B1860m further	"	"	"	5,20
"	"	"	B1781m	"	"	"	" (but ep.17, 30,31 & 32,M; ep. 20 in '-' stage
"	"	"	B1932f	"	"	"	"(ep. 20 in 'R' stage)
"	"	"	B1928f further	"	"	"	6
"	"	"	B1780m "	"	"	"	7,8,18,19(ep. 9 to 17 & 25 to 32,M)

Dental Age V.

In skel.	WRU,	B1930,m		"	"	"	3,5,6 (ep. 18 in '-',7,19 & 20 in 'B' & 8 in 'R' stage)

Dental Age V (Contd.)

In skel. WRU, B1425,m	further fusion of ep.	7,11,16,17?(M), 32?(M)(ep.18,19,20 in 'B' & 8 in 'R' stage)
" " AMNH, 90194	" " " "	8,9,18,19,20(ep. 13 to 17 & 27 to 32M)
" " WRU, B2742,f	" " " "	2,15 to 20,27 to 32(some ep. 29 in 'R' stage)
" " " B1764,f	" " " "	13 (ep.2 is in 'A' & 28 and some 29 in 'R' stage)
" " " B1953,f	" " " "	23,26 (ep. 2 is nil, 18 in 'B', 19 & 20 in 'R' stage)
" " " B1709,m	" " " "	22,24 (ep. 2 is ?)
" " " B2739,m	" " " "	10,21,25 (ep. 2 is ?)

Dental Age VI.

In skel. IM, m.g,C2,f	" " "	2,3,4,5 to 9,11,13 to 32 (ep. 10 is in 'R' and 12 in 'B' stage)
All other skeletons of this age show	" " "	2 to 11,13 to 32, 12 & 1.

On examination of the fusion occurring in the Dental Age stages as shown in the previous para, it is seen that epiphysial fusion does not run pari passu with tooth eruption sequence. For instance,

Skel. WRU B1931,m in Dental Age I shows fusion of ep. 3 & 5, but

Skel. WRU, B1753,m)
B1783,f) in Dental Age II shows fusion of ep. 3 only,
B1844,m) and
& B1935,m)

" " B1751,m " " " IV " " " " 3 only.

Ep. 20 fuses in 3 specimens out of 6 in Dental Age IV, but fails to fuse in 3 out of 10 in Dental Age V, in all of which again, fusion in many other epiphyses has taken place. Ep. 8 has fused in 1 out of 6 specimens in Dental Age IV, but has failed in 2 out of 10 in Dental Age V. Ep. 18 & 19 have fused in one out of eight specimens in Dental Age IV, but have failed in 3 out of 10 in Dental Age V. In the latter age ep. 10 is found fused in 1 out of 10 specimens but is in 'R' stage in 1 out of 42 of Dental Age VI.

It seems that ep. 5 vacillates slightly before entering on permanent fusion; ep. 8 also is a bit shaky in this respect; but there is considerable hesitation of ep. 18, 19 & 20, specially of ep. 20, before they are finally united. It should be remembered, however, that the epiphyses for medial epicondyle humerus and femoral trochanters (18,19 & 20) are extra-articular and as such their fusion is often erratic.

The union of ep. 5 is not of much consequence, since it occupies a very early position in the fusion scale. Ep. 18, however, a more constant and important member in the schedules given in previous pages, is definitely a variant in Gorillas. Ep. 11 (proximal ulnar or olecranon ep.), though extra-articular, behaves remarkably steadily in these animals.

Without reference to the dental age stages the S.E.F. in Gorillas may be represented, as had been done before in the case of other animals, as follows:-

In skel. WRU,	B1424,f, B1929,f, B1933,m; B1753,f, B1783,f, B1844,m B1935,m; & B1751,m	is seen fusion of ep.	3-
" " "	B1931,m, B1850,m , B1781,m & B1932,f	" " " " "	5
" " "	B1860,m	" " " " "	20
" " "	B1928,f	" " " " "	6
" " "	B1930,m	is seen fusion of ep.	6 (ep. 20 in 'R' stage)
" " "	B1425,m	" " " " "	7,11,16,17?, 32?, (ep.20 in 'B' stage)
" " "	B1780,m	" " " " "	8, 18, 19
" " AMNH,	90194	" " " " "	9
" " WRU,	B2742,f	" " " " "	2,15,27,28, some 29,30,31 (some ep. 29 in 'R' stage)
" " "	B1764,f	" " " " "	13 (ep. 2 in 'A', 28, and some 29 in 'R' stage)
" " "	B1953,f	" " " " "	14,23,26,29(all) (ep. 18 in 'B' 19 & 20 in 'R' stage ep. 2 nil)
" " "	B1709,m	" " " " "	22,24 (ep. 2?)
" " "	B2739,m	" " " " "	10,21,25(ep.2 ?)
" " IM,	m.g, C2,f	" " " " "	1,2,4 (ep. 10 in 'B' stage)
In all others of Dental Age VI		" " " "	12

Table No. 35

Order: PRIMATA Sub-order: Anthropoidea Sec: Catarrhini

s.	A n t h r o p o i d e a				
us	Anthropopithecus(Pan or Troglodytes or Chimpanzee)				
e	Pan	Pan	Pan	Pan	Chimpanzee
eum	W.R.U.	W.R.U.	W.R.U.	W.R.U.	W.R.U.
ber	B 830	B 829	B 1177	B 347	B 346
:	Male	Male			Male
	juv.	juv.	juv.	juv.	young
PIPHYSES					
lav, St.....	ct.	ct.	A	ct.	-
Ac.....	ct.	ct.	A	ct.	-
um, Pr.El..	B	B	B+	+?	+
" & Sh.	-	-	-	-	B-
Di.El..	-	-	-	B	+
" & Sh.	-	-	B	B	+
Lat.Ep.	-	-	ct.	-	+
Med.Ep.	-	-	-	-	B
ad, Prox...	B	B	ct.	B	- to B
Dist...	-	-	ct.	-	- to B
lna, Prox...	ct.	B	ct.	-	B
Dist...	ct.	-	ct.	-	-
:, First..	-	B	B	B	B
Rest...	-	B	B	B	-
(M),Prox...	-	B	B	B	- to B
Mid....	-	B	B	B	B
Term...	-	B	B	B	B
m, Head...	-	-	-	B	B
Gr.Tr..	ct.	-	-	B	B
Ls.Tr..	ct.	-	-	B	B
Dist...	-	-	-	-	- to B-
b, Con....	-	-	B	-	B-
Tb.....	ct.	-	B	ct.	B-
Dist...	-	-	B	B	- to B
b, Prox...	ct.	-	B	B	- to B
Dist...	-	-	B	-	B
lc. Epip...	-	B	B	-	B
, First..	-	B	B	B	B
Rest...	-	B	B	B	-
(P),Prox...	-	B	B	B	B
Mid....	-	B	B	B	B
Term...	-	B	B	B	B
t.Centre...					
L.FEATURE.	Many ep. marked '-' & some marked 'B' are covered by cartilage				
BITS ETC...					
ARKS......	Troch. ep. in ct.	Hd.hum. in ct.		Menageric ?	
NTITION....	M_1 out M_2 erupting	M_1 stage up. M_2 erupting	M_1 erupting	M_2 in M_3 not in	M_2 stage up. C. cutting

Table No. 36

Order: PRIMATA Sub-Order: Anthropoidea Sec: Catarrhini

- A n t h r o p o i d e a

Anthropopithecus (Pan or Troglodytes or Chimpanzee)

Pan	Pan	Pan	Pan	Pan	Pan
.U.A.	W.R.U.	W.R.U.	E.U.Z.	R.S.	W.R.U.
XXXII	B 2957	B 2773	RR 54	C,33	B 1426
		Female			Female
oung	young				
-	calcified	ct.	ct.	nil	A
t.	do.	ct.	ct.	nil	+
+	+	+	+	+	+
-	-	B-	-	B	B
+	+	+	R	+	+
R	+	+	R	+	+
R	+	+	R	+	+
B	B	+	R (in bits)	+	+
B	-	B+	R	+	+
-	-	B	-	B	R
R	B	R	R	+	+
-	-	B+	-	B	R
B	-	B	R	+	+
B	-	B	- to B	+	+
B	-	B	B to +	+	+
B	+	B	B	+	+
R	+	+	R	+	+
B	B	B	R	+	+
B	-	B+	+	+	+
B	B	+	R	+	+
-	-	B	-	R	R
-	-	B	-	R	R
-	nil	-	-	R	R
B	-	B	B	+	+
-	-	B	-	R	R
B	-	B	B	+	+
B	-	B	+	+	+
B	-	B	+	+	+
B	-	B	B	+	+
B	-	B	+	+	+
B	+	B	+	+	+
B	+	+	+	+	+
ep. at ²mt.V					
	ep. loose				approx. human age = 20 years. Lemur stage = 73
nd.	x	x	no skull	stand.	stand.

i.e., Proximal elements humerus
Distal elements humerus
(Lesser trochanter femur)
Distal epiphysis and shaft humerus
(Lateral epicondyle; proximal ulna); second and terminal phalanges, manus; terminal phalanx, pes
(Medial epicondyle and shaft humerus); head femur; (greater trochanter femur)
Proximal radius
Acromial epiphysis clavicle ? ; proximal phalanges, all; middle phalanx, pes; metatarsals; calcaneal epiphysis
Metacarpals; (tubercle of tibia); distal fibula
Distal tibia and proximal tibia
Proximal fibula; distal femur; distal radius
Proximal humerus; both epiphyses clavicle
Distal ulna

From a study of the above sequence, it will be seen that Gorillas, as compared with Cercopithecinae, Semnopithecinae and Platyrrhini, are peculiar in that the last limb epiphysis to fuse in them is the distal ulna. This has been fore-shadowed in Platyrrhini and Cercopithecinae and less so in Semnopithecinae (see supra).

Stevenson's schedule, therefore, fails to agree in these animals.

Genus Anthropopithecus (Troglodytes or Chimpanzee).

Very similar to but more completely arboreal than Gorilla. Fore-limbs reach but a slight distance below the knee. The manner of their walking is similar to that of the Gorillas.

35 skeletons were available for study. Of these 17 were adult and obtained as follows:-

EUA, 64XXXI, 64XXXIV; EUZ, BC,VI,4f; IM, m.g,C2; RS, C30 (comparative); WRU, B543f, B628f, B629m, B1056m, B1170m, B1195m, B1433m, B1434f, B1713f, B2730f, B2771f & B2823f.

Of the remaining 18 young specimens, skeletons WRU, B753, B880f, B1175, B1176, B1395 and EUA, 60LII were rejected from this study as they were very juvenile. The S.E.F. in the remaining 12 skeletons (Table Nos. 35 & 36) is as follows:-

In skel.	WRU, B347		fusion of ep.	3?
" "	EUA, 64XXXII		" " "	3, 5
" "	WRU, B346m	further	" " "	6, 7
" "	" B2773f	"	" " "	8,17,20,32
" "	" B2957	"	" " "	16,31 (8 & 20 in 'B' stage; sternal ep. is calcified)
" "	EUZ, RR54	"	" " "	some 15,19,27,28,30 (5 to 9, 11,13, some 15,17,18 & 20 in 'R' stage; 16 in 'B'stage)
(From skel " "		may be presumed further fusion of	"	9,11,13, some 15&18)
In skel.	RS, C35	"	" " "	9,11,13,14,15 (all), 18,20,24,26,29
" "	WRU, B1426	"	" " "	2(10,12,21,22,23 & 25 in 'R' stage; 4 is in 'B' stage & 1 in 'A')
From " "	"	may be presumed further fusion of	"	10,12,21,22,23 & 25
		followed by	" " "	4 & 1 which will fuse last.

in other orders of mammals.

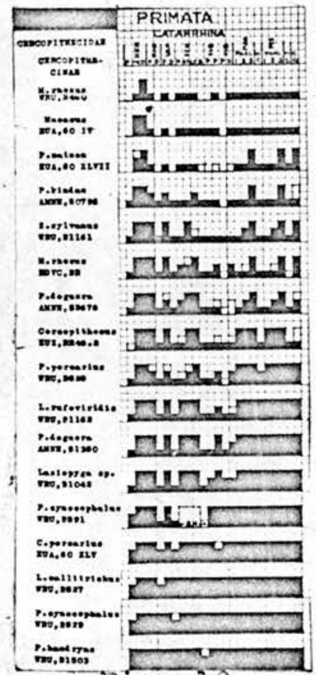


Fig. 19.
Epiphysial Chart
for Cercopithecinae.

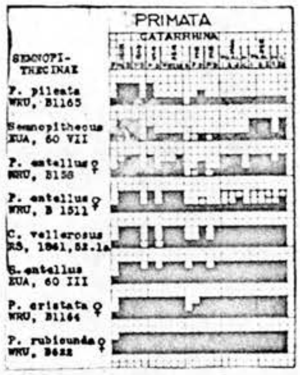


Fig. 20.
Epiphysial Chart
for Semnopithecinae.

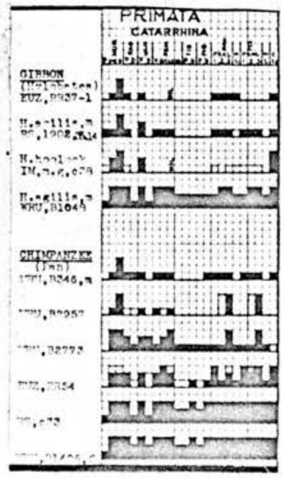


Fig. 21.
Epiphysial Chart
for Gibbon and
Chimpanzee.

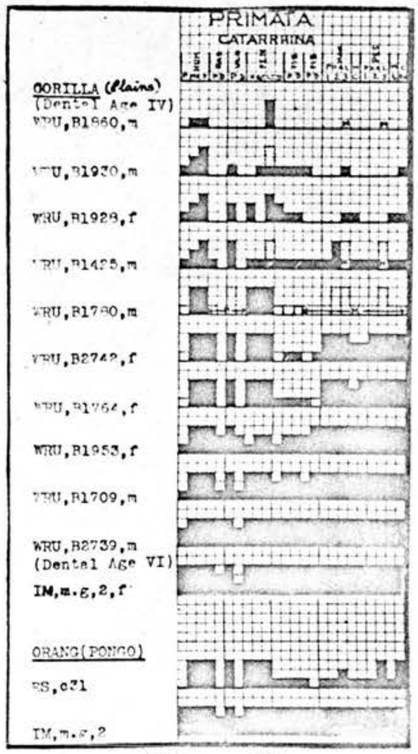
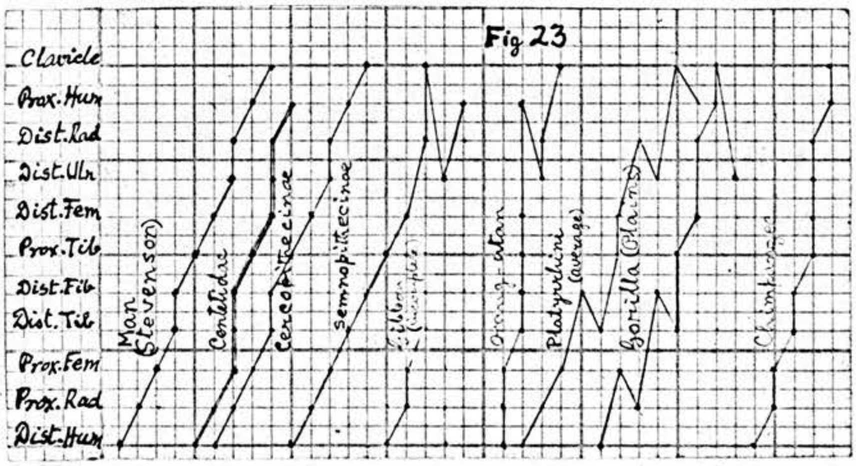


Fig. 22.
Epiphysial Chart for
Gorilla(Plains) and
Pongo(Orang-utan).

Note. Abbreviations same as in previous charts.

n other orders of mammals.

Fig. 23



Graph showing epiphysial fusion in the Catarrhine monkeys on the Stevenson scale. Graphs for Centetidae and Platyrrhina have been shown for comparison.

in other orders of mammals.

i.e., Proximal elements humerus
Distal elements humerus
Distal epiphysis (and lateral epicondyle) with shaft humerus
Terminal phalanges, all : (medial epicondyle, lesser trochanter femur)
Middle phalanges, all
Some proximal phalanges manus : first metatarsal : proximal phalanges pes : (greater trochanter femur, calcaneal epiphysis)
Proximal radius : Head femur : first metacarpals : some proximal phalanges manus : (proximal ulna)
Outer metacarpals : proximal phalanges manus, all : distal tibia : distal fibula
(Acromial epiphysis clavicle)
Proximal tibia : proximal fibula : distal radius : distal ulna : distal femur
Proximal humerus : (sternal epiphysis clavicle).

The sequence as given above has an implied close agreement with Stevenson's schedule though sufficient material was not available to sort out individual fusion specially of proximal radius, head femur, proximal tibia, fibula and humerus, distal radius, ulna and femur and sternal epiphysis of clavicle.

Epiphysial charts for Catarrhina (Figs. 19,20,21& 22) and graphs (Figs. 23) of the fusion of their epiphyses as compared with those of Centetidae and Platyrrhines etc. are attached.

DISCUSSION:

On reviewing the whole position in Primata, Lemuroidea and Insectivora, th primitive epiphysunion sequence may be considered to be that seen in unspecialised plantigrade terrestrial creatures like the Centetidae or Erinaceidae, in which, as simplified, it stands as follows:-

in other orders of Mammals.

<u>1st phase</u> Distal humerus, terminal and middle phalanges
Proximal radius; proximal phalanges
Head femur;
metatarsals; metacarpals;
distal tibia; distal fibula

<u>2nd phase</u> Proximal tibia; proximal fibula
Distal femur; distal radius; distal ulna
Proximal humerus

The above may be modified according to the special needs of the animal to fit it to new habitats and mode of progression. Thus,

1. <u>For an arboreal existence</u>:-

(i) If movements are <u>sluggish</u> and no great strain is placed on the paws, the fusion of phalangeal epiphyses is retarded, e.g., in Lorisinae (p.69) the sequence of epiphysial fusion is,

<u>1st phase</u> Dist. hum.;term. phals.; prox. radius
Head femur
Middle and proximal phalanges (all)
Metatarsals; metacarpals;
distal tibia; distal fibula

<u>2nd phase</u> Proximal tibia; proximal fibula
Distal femur
Distal radius; distal ulna;
proximal humerus

(ii) If movements are <u>brisk</u>:-

(a) The fusion of metatarsal and metacarpal epiphyses may be acclerated and that of head femur retarded,e.g

	Lemurinae	Galaginae	Chiromyidae	Cercopithecinae
1st phase	Dist. hum.	Dist. hum.;	As in	Dist. humerus
	Phals.(all);	phals.(all);	Galaginae?	Term. phals.
	prox. rad.;	prox. rad.;		Prox. radius
	metatarsals;	metatarsals;		Prox. & mid.
	metacarpals	metacarpals;		phals.(all)
	Head femur;	head femur;		Metatarsals
	eps. clav.	dist. tibia;		Metacarpals;
	Dist. tibia;	dist. fibula		head femur
	dist. fibula			Distal tibia
				Distal fibula

in other orders of mammals.

	Lemurinae	Galaginae	Chiromyidae	Cercopithecinae
2nd phase	Prox. tib.;	Prox. tib.;	Prox.tib.;	Prox. tibia
	prox. fib.	prox.fib.;	dist.fem.;	Dist. femur
	Dist. fem.	dist.fem.	dist.rad.;	Prox. fibula
	Dist. rad.;	Dist. rad.	dist.ulna;	Dist. radius;
	dist. ulna;	Dist.ulna;	prox.hum.	(eps. clav.)
	prox. hum.	prox.hum.	Prox. fib.	Dist. ulna
			Ep. clav.	Prox. humerus

In the 2nd phase, only proximal fibula is seen to be retarded slightly in Cercopithecinae and considerably in Chiromyidae. As mentioned before, this epiphysis is a variable one.

(b) Proximal radius may be accelerated and phalanges of manus retarded, as in Semnopithecinae (p.87). There may be slight change in the second phase as well, e.g., retardation of distal femur enabling the hind limbs to grow longer and afford a better leverage for taking long leaps.

(c) There may be retardation of distal humerus, e.g., in Tupaiidae (p.52).

(iii) In case of modifications of strain, the affected parts are seen to respond thus -

(a) The requisitioning of the tail as a prehensile organ takes off the strain from the phalanges, metacarpals and metatarsals, head femur etc., causing a retardation in part or whole of their sequences of fusion of epiphyses, thus -

Mycetinae.	Cebinae.
Distal humerus;	Distal humerus
terminal phalanges,(all);	Terminal phalanges, pes;
proximal phalanges (all);	proximal radius;
middle phalanx, manus;	distal tibia; distal fibula
head femur;	
distal tibia; distal fibula;	
proximal tibia; prox. fibula;	
distal femur	

in other orders of mammals.

Mycetinae.	Cebinae.
Metatarsals; metacarpals middle phalanx, pes; distal radius	Middle & prox. phalanges pes; head femur
Distal ulna	No further observations
Prox. humerus; eps. clav.	

Cebinae shows the largest amount of retardation, since the phalanges of manus are seen to have failed to fuse when those at the hip and ankle have already completed fusion. Further, the epiphyses of distal tibia and fibula have fused earlier than those at the hip, showing that in animals of this sub-family the strain of long leaps affects the ankles more than the hip. It may be that the original condition of the tail in the New-World monkeys was non-prehensile, as in the case of Old-World monkeys. The necessity for its prehensility having arisen, a transitional stage is manifested in the S.E.F. of Hapalidae before the stage of full-fledged prehensility is attended with the maximum divergence in S.E.F., as seen in Cebinae (pp. 78 & 79). Mycetinae is almost similar, though, for lack of material in the proper stage, it cannot be stated whether head femur fuses later than distal tibia and fibula. The middle phalanx pes, the metatarsals and the metacarpals are so much retarded in this sub-family that their fusion can be considered to be in the second phase, proving all the more the contention that prehensility of tail retards the fusion of epiphyses of bones near those joints that are normally involved in the act of prehensility.

In other Orders of Mammals.

Hapalidae shows the following S.E.F. (p.73) -

Distal humerus;
  terminal phalanges (all); proximal radius
Head femur; middle phalanx, pes
Proximal phalanx, pes
Distal fibula
Distal tibia; middle & proximal phalanges, manus;
  metatarsals; metacarpals; proximal tibia & fibula;
  distal femur, radius & ulna; epiphyses clavicle
Proximal humerus

This shows a retardation of all middle and proximal phalanges, specially those of manus, and of metatarsals and metacarpals as compared with the S.E.F. of non-specialised arboreals. Nyctipithecinae is a non-prehensile tailed sub-family of Cebidae, which contains all the prehensile-tailed monkeys. In the former, further retardation of terminal phalanges of pes is observed. In the prehensile-tailed Cebinae, terminal phalanges of manus in place of pes and head femur are retarded in addition, whereas in Mycetinae, the retardation affects the middle phalanges of pes, metatarsals and metacarpals.

(b) Volant modification takes away strain from elbow and hip; hence, distal epiphysis of humerus, proximal radius and head femur are retarded, as is seen in the S.E.F. in Galeopithecidae (p.56). Thus -

Phalanges all; metacarpals; metatarsals
Distal epiphysis humerus

2. In the Saltatorial type of progression on land:-

Retardation affects the metatarsals and the proximal and middle phalanges of pes more than those of manus (p. 52).

in other Orders of Mammals.

3. In Fossorial adaptation:-

Sufficient material is not available to show any special modification in the 1st phase (see p 54). The 2nd phase shows the S.E.F., as far as available (see p 56), to be

Proximal humerus : proximal fibula
Distal femur
Distal radius
Distal ulna

4. The Natatorial adaptation, as seen in Insectivora, implies wide modification. In Potamogalidae, metatarsals, metacarpals, distal tibia and distal fibula are apparently accelerated on account of retardation of head femur. Exactly the same is seen in Hylomys, which being a member of Erinaceidae should have generalised type of S.E.F. This shows the convergence of different types of S.E.F. according to functional similarity.

5. The assumption of semi-erect or erect posture in great apes and man:-

Excepting the Hylobates, the great apes possess heavy bodies and are less arboreal than other apes. They assume semi-erect posture in progression though they transfer some weight of their body to the knuckles or tips of their fingers. Gibbons "can walk erect; and when they do so, the big toe is separated as in unsophisticated or at least unbooted man"; at the same time they swing by means of the hand or branches of trees before taking long leaps. Hylobates material for study was very

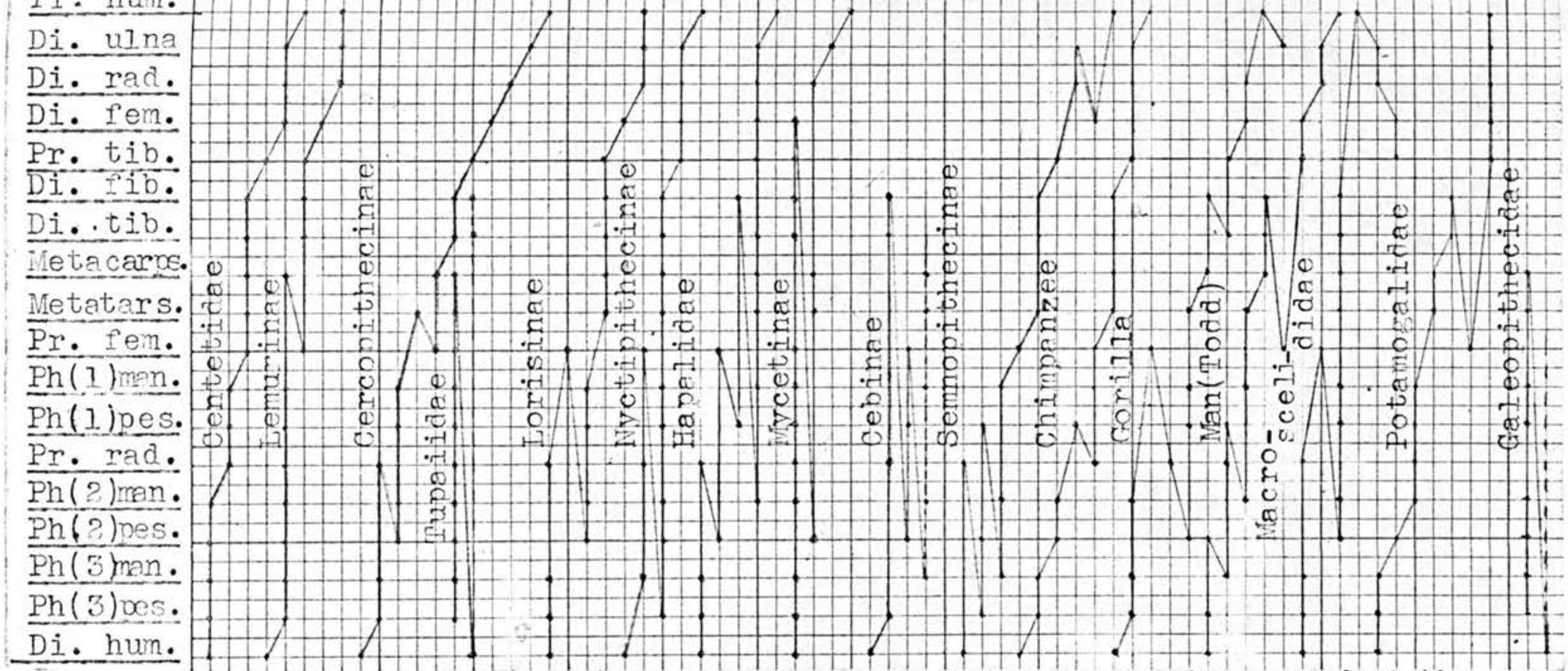
in other Orders of Mammals.

limited. It showed, however, retardation of epiphyses for all proximal phalanges, the fusion of proximal radius and femur being normal. Chimpanzee, Orang and Gorilla show various degrees of retardation in the order of epiphysial fusion on the typical Insectivora scale. In Chimpanzees some proximal phalanges of manus are retarded and metacarpals are accelerated relative to metatarsals. In Orangs, all phalanges of manus and middle and proximal phalanges of toes are retarded; proximal humerus is accelerated making distal ulna the last member to fuse. In Gorilla, all proximal phalanges of manus, proximal and middle phalanges of pes, proximal radius and slightly the distal tibia are retarded; proximal humerus is accelerated and distal ulna is the last to fuse. In Man, the proximal and middle phalanges of hand are retarded. The head femur is also retarded, thus providing for a relative acceleration of metatarsals, metacarpals, distal tibia and distal fibula. The proximal humerus, as in Chimpanzee, is the last to fuse apart from epiphyses of clavicle. There is therefore greater resemblence of the S.E.F. of Man with that of Chimpanzee than with Gorilla or Orang.

Thus it will be seen that there is, excepting minor differences, a convergence of S.E.F. in arboreal animals, e.g., Tupaiidae (Insectivora) ; Lemurinae, Galaginae and Chiromyidae (Lemuroidea) and Cercopithecinae and Semnopithecinae (Cercopithecidae). Removal of strain in different ways also brings

in other Orders of Mammals.

in other Orders of Mammals.



Graphs showing modifications in the Sequence of Epiphysial Fusion in different adaptations.

Terrestrial (i) Quadruped; no special adaptation - Centetidae.
(ii) Semi-erect; some phalanges of manus & head radius retarded - Chimpanzee, Gorilla.
(iii) Erect; phalanges 1 & 2 of manus retarded - Man.

Arboreal without modification of strain.

Brisk : (i) Metatarsals & metacarpals accelerated; head femur retarded - Lemurinae, Cercopithecinae
(ii) Proximal radius accelerated; phalanges of manus retarded - Semnopithecinae.
(iii) Distal humerus retarded - Tupaiidae.

Sluggish : Retardation of phalanges 1 & 2 - Lorisinae.

Arboreal with modification of strain.

(i) Tail prehensile; Retardation of some or all phalanges and/or metatarsals & metacarpals; acceleration of proximal radius and femur - Platyrrhini.
(ii) Volant (gliding) ; acceleration of metatarsals & metacarpals ; retardation of distal humerus, proximal radius & femur - Galeopithecidae.

Saltatorial ; Retardation of phalanges 1 & 2, proximal tibia & distal femur ; acceleration of proximal humerus - Macroscelididae.

Natatorial ; Marked retardation of proximal femur - Potamogalidae.

out a noticeable though not marked convergence in S.E.F. in imals so widely different as the sluggish Lorisinae (Lemuroi-a) and the non-prehensile-tailed Platyrrhini. The evolution intermediate forms may also be guessed from this study. nvergence in the sequence of fusion of epiphyses is also seen animals of different families taking to similar habitats, g., Potamogalidae and Hylomys (Erinaceidae). Though material not plentiful to do full justice to all modifications, yet has been possible to point to the existence of convergent aptations in divergent habitats. Thus in -

(a) Arboreal adaptations	-	Acceleration of metatarsals and metacarpals; retardation of distal humerus, or head or distal femur.
(i) Sluggish movements in arboreals	-	Retardation of proximal and middle phalanges of manus & pes.
(ii) Prehensile tail in arboreals	-	Retardation of phalanges of manus & pes, metatarsals & metacarpals.
b) Saltatorial adaptations	-	Retardation of middle & proximal phalanges, proximal tibia & distal femur; acceleration of proximal humerus.
c) Volant adaptations	-	Acceleration of metacarpals and metatarsals and retardation of distal humerus, proximal radius, proximal femur etc.
d) Natatorial adaptations	-	Marked retardation of head femur.

A graph (Fig. 23A) is attached to show the trend of S.E.F. in the adaptations mentioned above.

In the following pages will be seen how far the adapta-ons shown above may affect the sequence of epiphysial fusion other Orders of Mammals.

Table No.37
List of Rodentia studied.

ıb-order, ection, amily, enus &c.	Number of skeletons Total	Young	Adult	Habits, Special features &c.
<u>IMPLICIDENTATA</u>	54	47	7	
SCIUROMORPHA	10	8	2	Squirrel-like. Clavicles well-developed, fibula free.
Anomaluridae	2	2	-	Arboreal; limbs connected by patagium supported by a cartilage arising from olecranon process.
Sciuridae	8	6	2	Squirrels. Arboreal or terrestrial.
IYOMORPHA	18	16	2	Rat-like. Clavicles well-developed; tibia & fibula united.
Muridae	15	15	-	Pollex well-developed.
Spalacidae	1	1	-	
Dipodidae	2	-	2	Metatarsals greatly elongated and fused (cannon). Leap & burrow.
YSTRICOMORPHA	26	23	3	Porcupine-like.
Pedetidae	9	7	2	Hind-limbs elongated.
Octodontidae	2	2	-	
Hystricidae	5	4	1	
Erethizontidae	4	4	-	
Chinchillidae	2	2	-	
Dasyproctidae	1	1	-	
Caviidae	3	3	-	
<u>UPLICIDENTATA</u>	13	8	5	Manus five, pes four-toed.
Hares	3	2	1	
Rabbits	10	6	4	Shorter ears & legs than hares.
Total	67	55	12	

worn very slight wear - 0 1 3 1,0,1,3 1 0-1 3

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Table No. 38

Order: RODENTIA Sub-order: Simplicidentata Sec: Sciuromorpha

am	Anomaluridae		Sciuridae					
us	Anomalurus							
c	A.erythonotes	A.peacrofti	Xerus setosus	Protoxerus stanger	Sciurus coralinensis leucotis	S.vulgaris	Arctomys monax	Ratu. bicolor
eum	R.S.	W.R.U.	W.R.U.	R.S.	W.R.U.	E.U.A.	W.R.U.	R.S.
ber	1935 22.14	B813	B1359	1935 22.20	B2059	L23XXVI	B127	1870.7
		Young Adult			Male Young Adult		Juvenile	
PIPHYSES								
lav, St....	?	nil	B	?	A	nil	x	B
Ac....	nil	nil	B	?	+ or nil	nil	x	B
um, Pr.El.	+	+	+	R	+	+	+	+
" & Sh.	-	B	R	+	B	B	-	B_
Di.El.	+	+	+	+	+	+	+	+
" & Sh.	+	+	+	+	+	+	+	+
Lat.Ep.	+	+	+	+	+	+	-	+
Med.Ep.	+	+	+	+	+	+	-	B
ad, Prox..	+	+	+	+	+	+	-	+
Dist..	-	B	R	+	B	+	-	B
na, Prox..	+	+	+	+	+	+	-	+
Dist..	-	B	+	+	B	+	-	B
e, First.								
Rest..	+	+	+	B	+	+	-	+
a(M),Prox..	+	B+	+	R	+	+	-	+
Mid...	+	+	+	R	+	+	-	+
Term..	+	+	+	R	+	+	-	+
en, Head..	+	+	+	+	+	+	-	+
Gr.Tr.	+	+	+	+	+	+	-	+
Ls.Tr.	+	+	+	+	B	+	-	B
Dist..	R	+	+	+	+	+	-	B
b, Con...	+	+	+	+	+	+	-	B
Tb....	B	B	B	R	B	+	-	B
Dist..	-	B	B+	+	B	+	-	B_
b, Prox..	-	B	B+	+	B	+	-	B_
Dist..	B	B	+	+	+	+	-	B
lc. Epip..	-	B	M	+	B	+	-	B_
, First.	B	B	M	+	+	+	-	B
Rest..	+	+	+	+	+	+	-	+
(P),Prox..	+	B	+	R	+	+	-	+
Mid...	+	B	+	R	+	+	-	+
Term..	+	+	+	R	+	+	-	+
t.Centre..	+	+	+	+	+	+	-	+
L.FEATURE.	Cart. rod fr. clecr. for patagium		Verteb. ep. +					
BITS ETC..								
MARKS.....								
NTITION...	1,0,1,3 / 1,0,1,3	1.0.1.3 / 1 0 1 3 not much worn	1.0.2.3 / 1 0 ? 3 very slight wear	x	1.0.1.3 / 1 0 1 3	1.0.1.3 / 1 0 1 3	Upper M_3 not out 1.0.2.2 / 1,0,1,3	Upper M_3 not out 1.0.2.2 / 1 0 1 3

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THE STUDY OF EPIPHYSIS IN RODENTIA.

The Order Rodentia contains small to moderately large animals; plantigrade or semi-plantigrade; chiefly terrestrial; often burrow or live in burrows; some strong runners, some aquatic (voles), some arboreal (squirrels) and some volant (Anomaluridae). The range of their habitats is wide. They have no canines. The incisors grow from persistent pulp. In Sub-Order Simplicidentata there is only one pair of incisors in upper jaw. The Duplicidentata have two pairs in upper jaw. Clavicles are generally present.

Table No.37 shows a list of the animals studied.

SIMPLICIDENTATA:

This Sub-Order is divided into three sections (1) Scuiromorpha (squirrel-like); (2) Myomorpha (mouse or rat-like) and (3) Hystricomorpha (Porcupine-like).

Sciuromorpha.

1. In Anomaluridae (Table No.38) the following S.E.F. was seen in 2 specimens -

In Skel. W.R.U. B 813 ep. 3,5 to 9,11,13,15,16,17,27,30, 31,32 and 18,19 & 20.
" " R.S. 1935, 22.14 ... ep. 14,28,29 (19 is 'R') in addition.

2. In Sciuridae (Table No.38) the following S.E.F. was seen in 6 specimens -

In Skel. W.R.U, B 127 ... ep. 3,5,6
" " R.S,1870.7 further ... " 7,9,11,13,15 to 17, 27,30,31,32 & 14,28+29

much worn no wear slight wear

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In Skel. WRU,B 2059,m	further	...	ep. 8,19,20,24,26, 2
" " " B 1359	"	...	" 18,12
" " RS,1935,22.20	"	...	" 10,22,23,25 (13 to 16,28 to 30 are 'R'),1
" " EUA,L23XXVI	"	...	" 21
" " " "	presumably	..	" 4

Besides there were 2 adult specimens, one being S.vulgaris (EUA, L23XXVI) and the other Pteromys magnificans (IM,s.m.g).

The S.E.F. in the above two families may be arranged together as follows:-

3,5,6	i.e.	Prox. & dist. el. hum., dist. ep. with shaft hum.
7,9,11,13,15 to 17,27,30 to 32	"	Lat. epic. hum., prox. rad. & ulna, phal. manus, metacarp. of pollex, calc. ep., phal. pes.
14,28,29	"	outer metacarps, metatars.
(8), 19,20,2	"	Med. epic. hum., gr. & ls. trochs. fem. lat. ep. clav. (Med. epic. hum. is accelerated in Anomaluridae).
18	"	Hd. fem. (Prox. fem. is accelerated in Anomaluridae).
24,26	"	Dist. tib. & fib.
12	"	Dist. ulna
10,22,23,25,1	"	Prox. tib. & fib., dist. rad., st. ep. clav.
21	"	Dist. fem.
4	"	prox. hum.

Looking at Anomaluridae, the S.E.F. is found to be :-

much worn   no wear   slight wear

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Prox. & dist. el. hum.; dist. ep. & epic. with shaft hum.; phal. all; calc. ep.; prox. rad.; hd. & trochanters fem.; 1st metacarpels.

Outer metacarpals, metatarsals.

This shows an advancement of head and trochanters of femur over S.E.F. of Sciuridae. Whether or not the volant adaptation in Anomaluridae is responsible for this can be seen from a comparison with Galeopithecidae. The former is less characteristically volant, the patagium being very small; the flying of its members consists in alighting down small heights after getting there by climbing. As against Galeopithecidae, their metacarpals and metatarsals are very much retarded and head femur accelerated for a volant modification, though the distal humerus and proximal radius fuse normally. This type of S.E.F. compares favourably with that seen in non-prehensile-tailed fast arboreals like Tupaiidae. It may be presumed that the slight volant adaptation of anomalurus has not been sufficiently remote to have structural difference from a fast arboreal or resemblance with a more radically volant creature like the flying lemur.

Todd gives the S.E.F. in Sciuromorpha as follows:-

Terminal phalanges, manus & pes
Distal elements with shaft humerus
Acromial end of clavicle
Middle phalanges
Proximal Phalanx, manus

much worn — no wear — slight wear

Calcaneal epiphysis
Medial epicondyle humerus
Proximal radius
Metacarpals & metatarsals
Proximal phalanx, pes
Lesser trochanter, femur
Proximal ulna
Head, femur
Greater trochanter, femur
Distal tibia
Distal fibula
Distal femur
Proximal elements with shaft humerus
Proximal fibula
Proximal tibia
Distal radius
Distal ulna
Sternal epiphysis clavicle

Comparing the S.E.F. for Sciuromorpha as brought out in the present work with that given by Todd (as above), it will be seen that distal ulnar epiphysis and sternal epiphysis of clavicle are accelerated and distal femoral epiphysis is retarded in the former and proximal humeral is very much accelerated in the latter. Compared with the first and second spurts of fusion in Centetidae or with Stevenson's schedule, Todd's work shows acceleration, specially marked in proximal humerus and less so in distal femur. The present work, however, differs from Todd's results and is more in line with the schedule of fusion in generalized type of animals, excepting only very slight acceleration of distal ulna, distal radius and sternal epiphysis of clavicle.

much worn no wear slight wear

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Myomorpha - Clavicles usually well developed, tibia and fibula united.

Muridae - Pollex reduced.

The present study included 49 skeletons of albino rat from madder feeding experiments of Prof. Brash and 61 skeletons of castrated rats from the Genetics Laboratory of the Edinburgh University in connection with the work of Dr. Tang[42]. The last mentioned skeletons will be referred to in a later section. These two sets have not been shown in Table Nos.39 & 40.

The S.E.F., excluding manus and pes, in Prof. Brash's series is :-

3,5,6,7	i.e.	Prox. ele. hum., dist. el. hum. with shaft hum. and lat. epic. hum.
24	"	Dist. tib.
27, 9	"	Calc. ep., prox. rad.
26	"	Dist. fib.
8	"	Med. epic. hum.
20	"	Ls. tr. fem.

The S.E.F. in Dr. Tang's series, without manus and pes is :-

3,5,6,7,9,24,26	i.e.	Prox. el. hum., dist. el. hum. and same with shaft hum., lat. epic. hum.; prox. rad.; dist. tib.; dist. fib.
27	"	Calc. ep.
20, 8	"	Ls. tr. fem.; med. epic. hum.

Table No. 39

Order: RODENTIA Sub-Order: Simplicidentata Sec: Myomorpha

. Muridae

Mus decumanus E.U.Z. NN21 Fem.	Mus decumanus E.U.A. L23XXVI	Mus sp. W.R.U. B292	M.norwegicus albinus W.R.U. B594 Male Young adult	M.rattus R.S. 1894,13	M.norweg albinus W. R. U. B291 Male	Fiber zibethicus E. U.Z. BC,V3	F.zibethicus R. S. 1880,3.9	Otomys anchieta A.M.N.H. 86513 Fem.
Ct.	Ct,	M	M	B	B	A	B	B
?	Ct,	M	M	nil	A	nil	nil	nil
+	+	+	+	+	+	+	+	+
B	-	B	B	B	B	B	B	B
+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+
B+	+	+	+	R	+	R	+	+
+	+	+	+	+	+	+	+	+
B	-	-	B	B	B	-	B	B
+	+	+	B	R	+	R	+	B
B	-	-	B	B	B	-	B	B
Rud	Rud	Rud	Incomp.	Rud	M	Rud	Rud	Rud
+	+	x	"	+	M	R	+	+
+	+	x	"	+	M	R	+	+
+	+	x	"	+	M	R	+	+
+	+	x	"	+	M	+	+	+
+	+	+	R	S.H.	+	+	+	+
R	+	+	B	R	R	R	+	R
B	+	+	+	R	R	+	+	+
B	B	B	B	B	B	B	B_	B
B	-	B	B	B_	B	B	B	B
-	-	-	B	-	-	+	B	B
+	+	+	+	+	+	+	+	+
-	-	-	B	B_	B	B	B_	B
+	+	+	B	+	+	+	+	+
+	+	x	Incomp.	+	+	+	+	+
+	+	x	"	+	+	+	+	+
+	+	x	"	+	+	R -	+	+
+	+	x	"	+	+	+	+	+
+	+	x	"	+	+	+	+	+
+	+	x	"	+	+	+?	+	+
			Experimental animal					
		Fragmentary	signs of malnutrition	Hd.femur covered by glue	Fragmentary		-	
0.0.3 / 0 0 3	dm—present 1,0,0,3 / 10 0 3	1,0,0,3 / 1 0 0 3 much worn	1,0,0,3 / 1 0 0 3 no wear	1,0,0,3 / 1,0,0,3	1,0,0,3 / 1 0 0 3 slight wear	1,0,0,3 / 1 0 0 3	1,0,0,3 / 1 0 0 3	1,0,0,3 / 1 0 0 3

Table No. 40

Order: RODENTIA   Sub-Order: Simplicidentata   Soc: Myomorpha

	...ae (Contd.)					Spalacidae
...a .	O.anchieta A.M.N.H. 86506 Fem.	Arvicola amphibius E. U. A. L23XXVI	Hydromys chrysogaster W. R.U. B1358 Young adult	H.chrysogaster W.R.U. B294	Cricetomys gambianus W. R. U. B1356 Adult	Rhizomys Sumatranus W. R. U. B1360 Young adult
	?	B?	+?	B	B+	B
	nil	Ct.	+?	B?	+	Ct.
	+	+	+	+	+	+
	B	B	B	B	B+	B
	+	+	+	+	+	+
	+	+	+	+	+	+
	+	+	+	+	+	R
	+	+	+	+	+	B
	+	+	+	+	+	+
	B	B	B	B	B	B
	+	+	+	+	+	B
	B	B	B	B	B	B
	Rud	Rud	Rud	Rud	Rud	B
	+	+	+	+	+	B
	+	+	+	+	+	B
	+	+	+	+	+	B
	+	+	+	+	+	+
	+	+	+	+	+	B
	+	+	+	+	+	B
	+	+	+	+	+	B
	B	B	B	B+	B	B
	B	B	B	B	B	B
	B	B	B	B	B	B
	+	+	+	+	B	B+
	B	B	B	B	B	B
	+	+	+	+	+	B+
	+	+	B	+	+	M
	+	+	B	+	+	M
	+	+	B	+	+	M
	+	+	B	+	+	M
	+	+	B	+	+	M
	+	+	+	+	+	M
...s	Spec. ligamentous					
3/3	1.0.0.3 / 1 0 0 3	1.0.0.3 / 1 0 0 3	1.0.0.2 / 1 0 0 2 slight wear	1.0.0.2 / 1 0 0 2 much wear	1.0.0.3 / 1 0 0 3	1.0.0.3 / 1 0 0 3 considerable wear

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In 15 skeletons (Table Nos.39 &. 40) the S.E.F. is as follows:-

In Skel.	WRU, B594,m	...	ep. 3,5,6,7,8,9,20,24 (manus & pes missing)
" "	RS,1894,13 further	...	ep. 14 to 17, 26,27 to 32 (8 & 20'R' & 13 rud.)
" "	AMNH,86513,f "	... "	18
" "	WRU,B291,m,) FUZ,NN21,f &) AMNH,87066)	... "	11 (8 is 'B' & 20 'B' in EUZ, NN21,f & 20 is 'R' in WRU, B291,m)
" "	EUA,L23XXVI(M.decumanus)) WRU, B292,) RS, 1830, 3.9,) AMNH, 86506,F,) EUA, L23XXVI(A.amphibia)&) WRU, B294)	"	19
" "	WRU,B1358 &) " B1356) further	"	2; but in WRU,B1358 (aquatic)27 to 31 are 'B'
" "	EUZ,BC,V3 "	"	23 (8,11,14,15,16,19 & 29 are 'R')

<u>Spalacidae</u> - Only one specimen (Table No.40) was availed. It showed fusion of:-

Ep. 3,5,6,9,17 (pes Missing), i.e. prox. & dist. el. hum., latter & shaft, prox. rad, & term. phal. manus.

Proximal radius seems to be very early to unite in this case.

<u>Dipodidae</u> - 2 specimens, both fully adult (Table No.41) were available.

The S.E.F. for Myomorpha may therefore be recorded from the available data as follows:-

3,5,6,7,17,32 (?)	i.e.	Prox. & dist. el. hum., latter with shaft, lat. epic. hum. term. phal. manus & pes (?)
24	"	Dist. tib.
27, 9	"	Cal. ep., prox. rad.
26, (14 to 16, 28 to 31)	"	Dist. fib., (metacarpals, metatarsals, prox. & mid. phal.)
8	"	Med. epic. hum.
20	"	Ls. tr. fem.
18	"	Head fem.
11	"	Prox. ulna
19	"	Gr. tr. fem.
2	"	Lat. ep. clav.
23	"	Tub. tib.

NOTE:- Since manus and pes were not available in earlier specimens their epiphysial union has been placed within paranthesis from the stage when they were frist observed in the present series.

? indicates questionable presence or reading.

A very large amount of work has been done on the epiphysis of rats and mice by Todd[31] and his school and by Dawson (1925a[28] & b[77]). The order of epiphysial union recorded by them as compared with that found in this work is -

(a) For Mus decumanus, rattus, norvegicus albinus.

Todd[31]	Dawson(1925b)[77]	Present work
Phal. III, manus & pes	Hum., dist.	Hum., dist.
Phal. II, " "	Rad. prox.	Tib. dist.
Hum. dist.	Tib. dist.	(Rad. prox.
Fem., ls. tr.	Calc. ep.	(Calc. ep.
Tib. dist.	Fib. dist.	Fib. dist.

Todd[31]	Dawson(1925b)[77]	Present work
Fib. dist.	Hum., med. epic.	Hum., med. epic.
Rad. prox.	Ulna, prox.	Fem., ls. tr.
Clav. lat.	Fem., hd.	Fem., hd.
Phal. I, pes	Fem. gr. tr.	Ulna, prox.
Fem., Hd.	Fem., dist.	Fem., gr. tr.
Metacarp., metatars.	Tib. prox.	
Hum., med. epic.	Fib. prox.	
Calc. ep.	Rad. dist.	
Fem., gr. tr.	Ulna, dist.	
Clav., stern. end	Hum., prox.	
Fem. dist.		
Rad. dist.		
Ulna, dist.		
Tib., prox.		
Hum., prox.		
Fib., prox.		

(b) For Mus musculus

Todd[31]	Dawson[78]
Phal. III, manus & pes	Hum., dist.
" II, " "	Phal. I & II, manus
" I " "	" " ", pes
Hum., dist.	Rad. prox.
Rad., prox.	Tib., dist.
Tib. dist.	Metacarpals
Metacarpals	Metatarsals
Metatarsals	Calcaneal epiphysis
Calcaneal epiphysis	Ulna, prox.
Fem., ls. trochanter	Fem., gr. trochanter
" hd.	Fem., hd.
Hum., med. epic.	Fem., dist.
Ulna, prox.	Hum., prox.
Fem. gr. trochanter	Tib., prox.
" dist.	Fib., prox.
Hum., prox.	
Tib., prox.	
Fib., prox.	
Rad. dist.	
Ulna, dist.	
Fib., dist.	
Clavicle	

(c) For Myomorpha, as a whole,

Todd[31]	Present work.
Phal. III, manus & pes	Hum., dist.)
Hum., dist.	Tib., dist.) Phal. I,II,III;
Phal. II, manus & pes	Calc. ep.) Metacarpals;
Clav. lat.	Rad., prox.) Metatarsals
Tib. dist.	Fib., dist.)
Fib.,dist.	Hum., med. epic.
Fem., ls. tr.	Fem., ls. trochanter
Phal. I, manus & pes	Fem., hd.
Calcaneal epiphysis	Ulna, prox.
Metacarps. & Metatars.	Fem., gr. trochanter
Fem., hd.	Clav., lat.
Fem., gr. trochanter	Tib., prox. (tubercle only)
Hum., med. epic.	
Rad., prox.	
Fem., dist.	
Ulna, prox.	
Clav., sternal end	
Fib., prox.	
Tib., prox.	
Hum., prox.	
Rad., dist.	
Ulna, dist.	

Comparing the data obtained for Myomorpha in the present work and supplementing it from Todd's work, it is found that, though terrestrial and plantigrade and partly fossorial, the S.E.F. in Mymorpha differs from the schedule for generalised type of mammals as given before (see Insectivora) in that during the first spurt, marked acceleration in fusion of epiphyses at ankle (distal tibia & fibula) and slight retardation in that of medial epicondyle humerus occur in Myomorpha. The second spurt is characterized by acceleration of fusion of proximal humeral and retardation of distal radial and ulnar

Table No. 41

Order: RODENTIA Sub-Order: Simplicidentata

yomorpha See: Hystricomorpha

podidae		Pedetidae						
culus culus R.S. 1938, 18	Dipus aegyptiacus R.S. 1872, 20.8	Taterona valida A.M.N.H. 86508 young	T.valida A.M.N.H. 86515 Male young adult	T.valida A.M.N.H 86536 young adult	T.valida A.M.N.H 86532 Female young adult	T.valida A.M.N.H 86530 Female young adult	T.valida A.M.N.H 86511 Female young adult	T.valida A.M.N.H 86589 adult
S.H	+ or nil	M	A	B	B	?	B	+
S.H	do.	M	?	B	?	B	?	+
+	+	+	+	+	+	+	+	+
+	+	-	B	B	-	B	R	+
+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+
+	+	B	R	+	+	+	+	+
+	+	+	+	+	+	+	+	M
+	+	-	B	B	B	B	R	M
+	+	B	R	R	+	+	+	+
+	+	-	B	B	B	B	R	+
+	+	?	+	?	?	+	+	+
+	+	?	+	?	?	+	+	+
+	+	?	+	?	?	+	+	+
+	+	?	+	?	?	+	+	+
+	+	?	+	?	?	+	+	+
+	+	B	+	+	+	B	+	+
+	+	B	R	+	+	B	+	+
+	+	B	R	+	+	B	+	+
+	+	B	B	B	B	R	+	+
+	+	-	B	B	B	B	+	+
+	+	-	B	B	-	B	+	+
+	+	+	+	+	+	+	+	+
+	+	-	B	B	B	B	+	+
+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+
+	nil	Rud	Rud	Rud	?	Rud	Rud	Rud
+	+	+	+	+	?	+	+	+
+	+	+	+	+	?	+	+	+
+	+	+	+	+	?	+	+	+
+	+	+	+	+	?	+	+	+
icate men, under micros.		sp.ligamentous		sp.ligamentous	sp.ligamentous			
,0,3 / 03	1,0,0,2 / 1003	1,0,1,2 / 1012	1,0,1,2 / 1012	1,0,1,2 / 1012	1,0,12 / 1012	1,0,1,2 / 1012	1,0,1,2 / 1012	1,0,1,3 / 1013

epiphyses almost exactly as are seen in the burrowing Chrysochloridae. Stevenson's schedule for man and his theory referred to before do not hold in the present case.

Dawson's[79] assumption that certain epiphyses e.g. proximal humerus and distal femur, never fuse in rats has been challenged by Todd, who attributes Dawson's failure to observe fusion in such epiphyses to his work being done mainly on Laboratory-bred animals. Todd maintains and the present work also shows that in wild rats none of the limb epiphyses ever fails to fuse.

<u>Hystricomorpha</u> - Porcupine-like. Clavicles perfect or imperfect. Fibula distinct.

<u>Pedetidae</u> - 7 young (Tables Nos. 41 & 42) and 2 adult (Taterona valida, AMNH, 86589 & Pedetes kaffer, RS.C27) skeletons were examined. The hind limbs of these are elongated and the metatarsals are free.

The following is the S.E.F. :-

In Skel.	AMNH,		86508		...	ep. 3,5,6,7,9 (13 to 17? ligt.)24,26,27,29 to 32
"	"	"	86530,f,further		...	" 8,11,13 to 17
"	"	"	86515,m	"	...	" 18 (8 & 11 in 'R' stage)
"	"	"	86536 & 86532,f	"	...	" 19,20(11 in 'R' stage in 86536, & manus & pes ligt. in 86532,f)
"	"	"	86529,m	"	...	" 21, 1, 2
"	"	"	86511,f	"	...	" 22,23,25 (10,12 & 4 in 'R' stage; 1 in 'B' stage)
"	"	"	"			will presumably show fusion of 10,12 & 4 to be followed by 1

The above, therefore, will show the following sequence in Pedetidae:-

Proximal and distal elements humerus : distal epip. & lat. epicondyle with shaft humerus : Proximal radius : (metacarpals & phalanges of manus ?): metatarsals & phalanges of pes : distal tibia & fibula.

Lat. epicondyle humerus : prox. ulna : all epiphyses of manus.

Head femur.

Trochanters femur.

Distal femur : lat. ep. clavicle : (st. ep. clav?)

Proximal tibia & fibula.

Distal radius & ulna : proximal humerus.

St. ep. clavicle (?)

NOTE:- In P. kaffer, RS, C27, all limb epiphyses, including those of clavicles, were united and there was a free ossicle articulating with the lateral end of clavicle.

Octodontidae - Clavicles complete. Manus and pes usually pentadactyle. Terrestrial, Occasionally fossorial.

2 specimens were availed for study (Table No.42), showing -

In Skel. EUZ, NN29.2 fusion of ep. 3,5,6,9,15,16,17,23,24,26, 27,28,30,31,32; and
" " WRU, B697 further fusion of ep. 7,8,13,14,20,29 (23 is '-' & 27 'R')

The sequence therefore is :-

Proximal & distal elements and distal epiphysis with shaft of humerus : proximal radius : phalanges (all) : first metatarsals : distal tibia and fibula : calcaneal epiphysis.
Epicondyle humerus : metacarpals, outer metatarsals ; lesser trochanter femur.

Table No. 42

Order: RODENTIA Sub-order: Simplicidentata Sec: Hystricomorpha

idae		Octodontidae		Hystricidae					
ig- AH- ei N.H	Pedetes kaffer R.S.	Aulacodas swinderinas W.R.U.	Myocastor coypus E.U.Z.	Porcupine E.U.A.	Trichys lipura W.R.U.	Hystrix cristata W. R. U.	H. leucura R.S.	Porcupine E.U.A.	.cho pa- lo- is .U.
9	27	B 697	NN29.2	L23III juvenile	B264	B1045	27, 1836	L23V	7
	+	B	B	nil	nil	M	nil	C.ct	
	+	ct	B	"	"	M	"	"	
	+	+	+	-	+	+	+	+	
	+	B	B	-	-	B	R	+	
	+	+	+	+	+	+	+	+	
	+	+	+	-	B	+	+	+	
	+	+	R	-	B	+	+	+	
	+	+	B_+	-	B	+	+	+	
	+	+	+	-	B	+	+	+	
	+	B	B	-	B	B	+	+	
	+	B	R	-	B	B	+	+	
	+	B	B	-	B	-	+	+	
	+	+	R	nil	+	B_+	+	+	
	+	+	R	-	B	B_+	+	+	
	+	+	+	-	B	+	+	+	
	+	+	+	-	B	+	+	+	
	+	+	+	-	+	+	+	+	
	+	B_+	R	-	B	B_+	+	+	
	+	B_+	B_+	-	B	B_+	+	+	
	+	+	B	-	B	B_+	+	+	
	+	B	B	-	B	B	R	+	
	+	B_-	B	-	B	B	R	+	
	+	B_-	+	-	B	B	R	+	
	+	+	+	-	B	R	+	+	
	+	B_-	-	-	B	-	R	+	
	+	+	+	-	B	B	+	+	
	+	R	+	-	B	+	+	+	
d	Rud	nil	+	rud	B	+	+	+	
	+	+	B_+ to R	-	B	+	+	+	
	+	+	R to +	-	B	+	+	+	
	+	+	R to +	-	B	+	+	+	
	+	+	+	-	+	+	+	+	
	a free ossicle articulating with lat. ep. of humerus		3rd phalanx covd. by claw		pisiform has an epiphysis at free surface Arboreal				287
a- s									
3 / 3	1.0.1.3 / 1 0 1 3	1.0.1.3 / 1 0 1 3	1.0.1.3 / 1 0 1 3	$\frac{di_1 I_1}{di_1 I_1}, C\frac{0}{0}\frac{P_1 dm_1}{P_1} M\frac{1,2,3}{1,2,3}$	1.0.1.3 / 1 0 1 3 much worn	1.0.1.3 / 1 0 1 3 much worn	1.0.1.3 / 1 0 1 3	1.0.1.3 / 1 0 1 3	1. worn

Hystricidae - Clavicles incomplete. Limbs sub-equal.

4 young specimens (Table No.42) and 1 adult (Porcupine, EUA, L23V) were studied. The fusion observed was as follows:-

In Skel.	EUA, L23III,	...	ep.	5
" "	WRU, B264	further fusion of	ep.	3,13,17,32
" "	" B1045	" "	" "	6,7,8,9,15,16,27 to 31
" "	RS, C27,1836	" "	" "	11,14,18,19,20,24,26, 10,12
" "	EUA, L23V	" "	" "	4,21,22,23 & 25 (1 & 2?)

The above reading gives the following sequence :-

Distal elements humerus
Proximal elements humerus : first metacarpals : terminal phalanges (all)
Distal epiphysis & both epicondyles with shaft humerus : proximal radius : proximal and middle phalanges : calcaneal epiphysis : metatarsals.
Proximal ulna : outer metacarpals : head & trochanters femur : distal tibia & fibula : distal ulna & radius.
Distal femur : proximal tibia & fibula : proximal humerus.

NOTE:- Clavicles being incomplete their epiphyses cannot be placed in the above list.

Erethizontidae - Clavicles complete.

4 specimens were studied (Table No.43). Their S.E.F. was as follows:-

In Skel.	WRU, B1287,m	there was fusion of	ep.	3,5,6
" "	RS, C26	there was further	" " "	7,17 (32 was 'R')
" "	WRU, B1133,f	" " "	" " "	8,9,11,32
" "	" B263	" " "	" " "	13 to 16, 18,19, 20,24,26,27 to 31

The above indicates the following sequence :-

Proximal & distal elements humerus: distal epiphysis & shaft humerus.

Lateral epicondyle humerus : terminal phalanges manus.
Medial epicondyle humerus : proximal radius : proximal ulna : terminal phalanges pes.
Proximal & middle phalanges (all) : metacarpals and metatarsals : proximal femur (all) : distal tibia and fibula.

NOTE:- In E. dorsatus (RS, C26) many phalanges of manus and pes did not show the presence of an epiphysis. In E. dorsatus (WRU, B1133,f) though the terminal phalangeal epiphyses seem to be completely fused, yet the amount of glazing found at epiphysial sites left one in considerable doubt as to whether there had really been any epiphysis at these sites, though the analogy of the middle and proximal rows of phalanges would lead one to think that such might have been present. The observation made on the specimens in the R.S. Museum however confirms the suspicion recorded in the case of the latter specimen.

Chinchillidae - Terrestrial. Complete clavicles. Long hind limbs.

The 2 specimens studied (Table No.43) showed the following:-

In Skel. RS, 1881, 3.11 there was fusion of ep. 3,5,6,7,9 (13 nil),20,24, 26,27 (28 nil), 29 to 32

" " RDVC, BR, there was further " " " 11,18,19,23(8 is 'R')

i.e. the S.E.F. is :-

Proximal & distal elements humerus : dist. ep. & lat. epic. with shaft hum. : prox. rad. : manus & pes (all) : ls. tr. fem. : dist. tib. & fib.
Prox. ulna : head & gr. tr. fem. : tub. tibia.

Dasyproctidae - Pes has three digits.

Only one specimen studied (Table No.43). It showed fusion of medial epicondyle of humerus in addition to those seen in Chinchillidae.

Table No. 43

Order: RODENTIA Sub-order: Simplicidentata Sec: Hystricomorpha

...thizontidae				Chinchillidae		Dasyproctidae	Caviidae		
...dor-satus W.R.U. ...287 ...le ...yr.	E.dorsatus R.S. c.26	E.dorsatus W.R.U. B1133 Female young	Cercolabes pr. W.R.U. B263	Viscacia viscacia R.S. 1881.3.11	Lagostomus sp. RDVC B.R. Male	D.prymnolopha R.S. c.26	Hydrochoerus capybara I.M.,smg 4008	H.capybara R.S. 1876.55.4	Dolichotis patachonicus W.R.U. B 267
l	x	G	nil	B	M	nil	nil	nil	nil
.	x	G	"	ct.	M	"	"	"	"
	+	+	+	+	+	+	+	+	+
	-	B	B	-	B	-	-	B+	B
	+	+	+	+	+	+	+	+	+
	+	+	+	+	+	+	B	+	+
	+	+	+	+	+	+	B	+	+
	B	+	+	R	R	+	B	+	+
	B	+	+	+	+	+	+	+	+
	-	B	B	-	-	B	-	-	B+
	B	+	+	R	+	+	B	R	+
	-	B	B	-	-	B	-	-	B
	-	B	+	nil	nil	+	nil	nil	nil
	-	B	+	+	+	+	-	+	+
	B to nil	B	+	+	+	+	B	+	+
	B to nil	B	+	+	+	+	B	+	+
H	+	+	+	+	+	+	+	+	+
Rt.	Lt.	B+	+	B	+	+	B	+	+
B	=	B+	+	R	+	+	B	+	+
B	ct.	B+	+	+	+	+	B	+	+
-	-	B	B	-	B	B	-	B	B
-	-	B	B	-	B	B	-	B+	B
-	-	B	B	-	+	B	-	B	B
B	-	B	+	+	+	+	B	+	+
-	-	B	B	-	-	B	-	-	B.
B	-	B	+	+	+	+	B	+	+
	- to B	B	+	+	+	+	B	+	+
	-	B	+	nil	nil	nil	nil	nil	nil
	-	B	+	+	+	+	-	+	+
	nil to -	B	+	+	+	+	B	+	+
	nil to B	B	+	+	+	+	B	+	+
H.	R to +	+	+	+	+	+	+	+	+
unites ...p.5 & hum.	not all phalanges have eg.			long hind limbs			op.on free sari.pisi-form; ep.8 same as in WRU,B1287; Forrestrial or Aquatic		
...n-...ated							skel.articulated		
Hard wear	std.	std. sl.wear	std. much worn	std.	std.	std.	std.	std.	std. much worn

Caviidae - Terrestrial or aquatic.

3 specimens were studied (Table No.43), 2 being aquatic (Hydrochoerus) and one terrestrial. The epiphysial fusion is shown below:-

In Skel. IM, s.m.g, 4008 ep. 3,5,9,17,32
" " RS,1876, 35.4 ep. 6,7,8,(13 nil)14,15,16,18,19,20, 24,26,27 to 31 (28 nil)
" " WRU, B267 ep.11

Not enough earlier or later specimens were available to show whether the terrestrial or aquatic habits of the animals would induce any change in epiphysial fusion. Zuck,[80] however, undertook a special investigation of epiphysis on 55 male and 62 female unrelated guinea-pigs. The S.E.F. of guinea-pigs as observed by Zuck and that of Caviidae as found in the present work are given below.

S.E.F. for Guinea-pigs (Zuck)	S.E.F. for Caviidae
Dist. hum.	Prox. & dist. el. hum.; prox. rad.; terminal phal.
Mid. phal., manus & pes	Dist. ep. & both epic. hum.; prox. & mid. phal.; metacarps & metatars; prox. fem; dist. tib. & fib.
Prox. fem.	Prox. ulna
Prox. phal. manus & pes	
Metatars II, prox. rad.	
Calc. ep.;metacarps I,II,III	
Dist.tib.;metatar I,III; IV	
Dist. fem.	
Prox. hum.	
Dist. fib.	
Prox. ulna	
Dist. rad.	
Prox. tib; dist. ulna	
Tub. tibia	

Zuck's work on guinea-pigs was a very thorough one. It consisted of (i) a study by dorso-ventral and lateral radiograms of macerated skeletons checked repeatedly against similar radiograms on the living, (ii) a macroscopic study of

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e skeletons themselves and (iii) checking of the results dependently by 3 well-trained observers. It will be seen that ck's result differs widely from that of Stevenson, proving ce again that the same schedule of S.E.F. would not hold iversally.

An analysis of the epiphysial fusion in the families of stricomorpha available for study for this work is given low along with the sequence recorded by Todd in his published work[31] on the 'Epiphysial Union in Mammals with ecial reference to Rodentia'. The material in the present ries being much smaller than what Todd and his co-workers d availed of, it is not possible to claim the same volume work or attain to the same strength of argument as was ssible for Todd to achieve. The present work however dicates a small retardation in fusion of epiphysis of rminal phalanges and head and greater trochanter femur; and considerable retardation in that of medial epicondyle merus and sternal epiphysis clavicle. The epiphyses for stal humerus, distal tibia, distal fibula and proximal dius are all seen to be accelerated. Todd's findings agree th Stevenson's Table in the fusion of epiphysis for medial icondyle humerus, proximal femur, distal tibia and fibula, t do not agree in that for proximal ulna, distal femur, oximal humerus and clavicular epiphyses; proving again the tenability of formulating any dogmatic law of epiphysial sion that will hold for all animals and for all times. The tter observation is further supported by Zuck's excellent work.

---- ---- ----- ---- much worn

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Fig. 24.
Epiphysial Chart
(Sciuromorpha & Myomorpha)

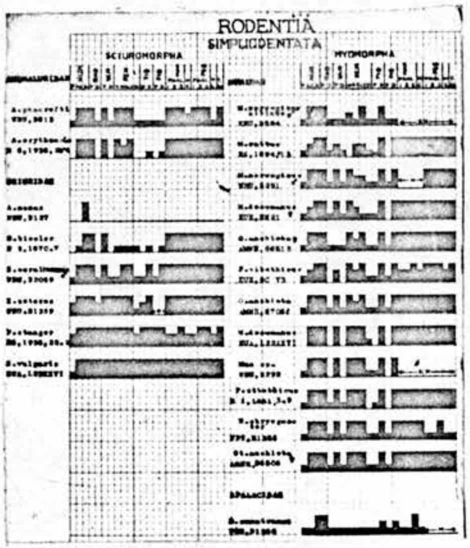

Fig. 25.
Epiphysial Chart
(Hystricomorpha)

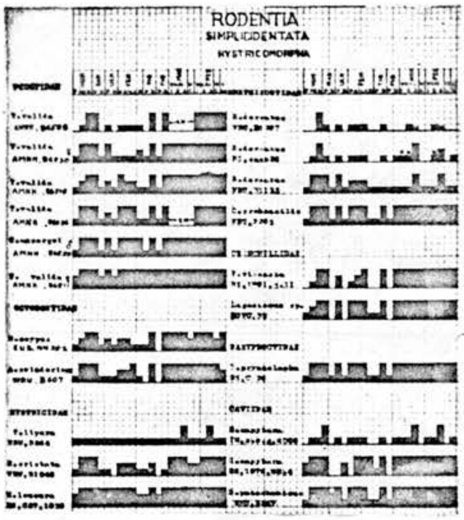

Fig. 26.
Group-pattern of E.U.S in Rodents

Fig. 27.
Terminal variations in Group-pattern

Note. All abbreviations are as in previous charts.

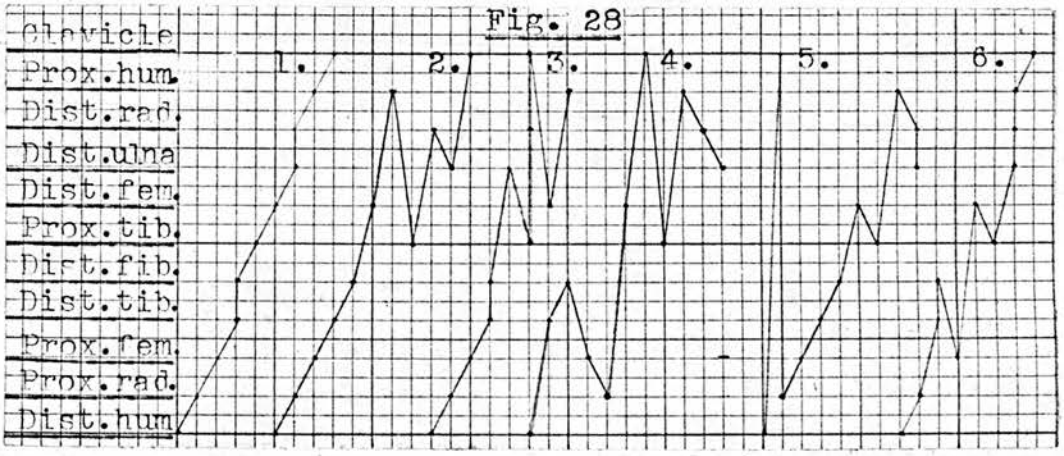

Fig. 28.

Graphs showing Sequences of Epiphysial Fusion :

1. Man (Stevenson). 2. Sciuromorpha (Todd).
3. Sciuridae (Basu). 4. Myomorpha (Todd).
5. Hystricomorpha (Todd). 6. Hystricomorpha (Basu).

Order of Epiphysial fusion in Hystricomorpha (average).

Todd[31]

Phal. III, manus & pes
Hum., dist.
Phal. II, Manus & pes
Hum., med. epic.
Clav., lat.
Clav., sternal
Calc. ep.
Rad. prox.
Metacarpals & metatarsals
Femur, ls. tr.
Femur, head
Femur, gr. tr.
Tib., dist.
Fib., dist.
Ulna, prox.
Femur, dist.
Tibia, prox.
Fib., prox.
Hum., prox.
Rad., dist,
Ulna, dist.

Present work.

Hum., dist. el.
Hum., prox. el.
Hum., dist. ep. & shaft (except in Hystricidae & Caviidae)
Hum., lat. epic. (except in Octodontidae, Hystricidae and Caviidae)
Phal. III, manus & pes
Rad., prox.
Phal. I, II (all) : Cal. ep. : metatarsals (except in Octodontidae)
Metacarpals : fem., ls. tr. (except in Pedetidae) : dist. tib. : dist. fib.
Hum., med. epic. (accelerated in Hystricidae, Erethizontidae & Caviidae ; retarded in Chinchillidae)
Fem., head & gr. tr. (retarded in Pedetidae)
Fem., dist.
Tib., prox. : Fib., Prox.
Rad., dist. : ulna, dist. (accelerated in Hystricidae): hum., prox.
Clav., sternal end.

Figs. 24 & 25 show the Epiphysial Charts for Sciuromorpha, Myomorpha and Hystricomorpha. Figs. 26 and 27 give the Group-pattern and the terminal variations. Fig. 28 shows the graphical position on the Stevenson-scale.

much worn much worn much worn

Table No. 44

Order: RODENTIA Sub-order: Duplicidentata

Lepus domesticus W.R.U. B538 young adult	Rabbit RDVC B.R. Fem. young	L. domesticus W.R.U. B2152 Fem. adolescent	L. domesticus W.R.U. B539 Male full grown	Hare E.U.A Comp.	Lepus W.R.U B2178	Rabbit E.U.A. L23XIII	Hare ? E.U.A. L23VII	Rabbit E.U.A. Comp.
nil	M	A	nil	x	M	M	x	x
nil	M	Q	nil	x	M	M	x	x
+	+	+	+	+	+	+	+	+
-	-	B	B	B	R	+	R	+
+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+
+	+	+	+	+	M	+	+	+
-	-	R	+	+	M	+	+	+
R	+	+	+	+	M	+	+	+
-	-	R	+	+	M	R	+	+
to +	R	+	+	+	+	+	+	+
do.	R	+	+	+	+	+	+	+
do.	+	+	+	+	+	+	+	+
do.	+	+	+	+	+	+	+	+
do.	+	+	+	+	+	+	+	+
B	R	+	+		+	+	+	
-	B to R	+	+		+	+	+	
-	B	+	+		+	+	+	
-	-	B+	+		R	+	+	
-	-	R	R		+	+	+	
-	-	+ (part. l.u)	+ (part. l.u)		+ (part. l.u.)	+	+	
R	+	+	+		+	+	+	
-	-	B+	+		+	+	+	
R	+	+	+		+	+	+	
to +	+	+	+		+	+	+	
do.	+	+	+		+	+	+	
do.	+	+	+		+	+	+	
do.	+	+	+		+	+	+	
do.	+	+	+		+	+	+	
do.	+	+	+		+	+	+	
x	x	2.0.3.3 / 1 0 2 3 much worn	2.0.3.3 / 1 0 2 3 much worn		2.0.3.3 / M much worn	2.0.3.3 / 1 0 2 3	2.0.3.3 / 1 0 2 3	

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DUPLICIDENTATA:

Fibula ankylosed to tibia ; manus has 5 and pes has 4 digits.

13 specimens of hares and rabbits were studied. 9 have been shown in Table No.44. The remaining 4 were adults specimens as follows:-

WRU, B283, B2177 & B2179 ; & RS, 1936, 39.3

The S.E.F. in the young specimens was as follows:-

In Skel.	WRU, B538	fusion	was seen	in ep.	3,5 to 9, 13 to 17 & 27 to 32
" "	RDVC, BR,f	"	continued	" "	11, 24
" "	WRU, B2152,f	"	"	" "	18,19,20,23 (L.U)
" "	" B539,m &) EUA, hare,comp)	"	"	" "	10,12,21,25
" "	WRU, B2178,	"	"	" "	22 (21 was 'R')
" "	EUA, L23VII	"	"	" "	22, (21 was ' ' & 4 was 'R')
" "	EUA, L23XIII	"	"	" "	4 (12 was 'R')

The above sequence compared with Todd's findings can be represented as follows:-

Todd[31]	Present work
Phal. III, manus & pes Hum., dist. Hum., med. epic. Phal. II, manus & pes Rad., prox. Calc. ep. Phal. I, manus	Prox. & dist. el. hum. : phal. III, manus & pes : dist. ep. & lat. epic. with shaft hum: med. epic. hum. : phal. II (all) : rad. prox. : calc. ep. phal. I (all) : metacarpals & metatarsals.
Ulna, prox.	Ulna, prox. : tib., dist.
Fem., ls. tr.	Fem., hd. : Fem., trs. : tub. tib.
Phal. I, pes Metacarpals & metatarsals Tib., dist.	Fem., dist. : fib., prox. & rad. dist. : ulna, dist.

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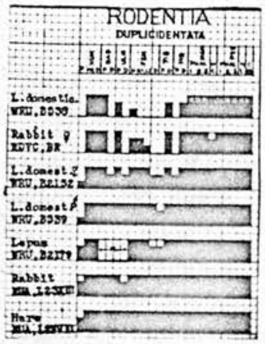

Fig. 29.
Epiphysial Chart
for Duplicidentata.
Abbreviations same as before.

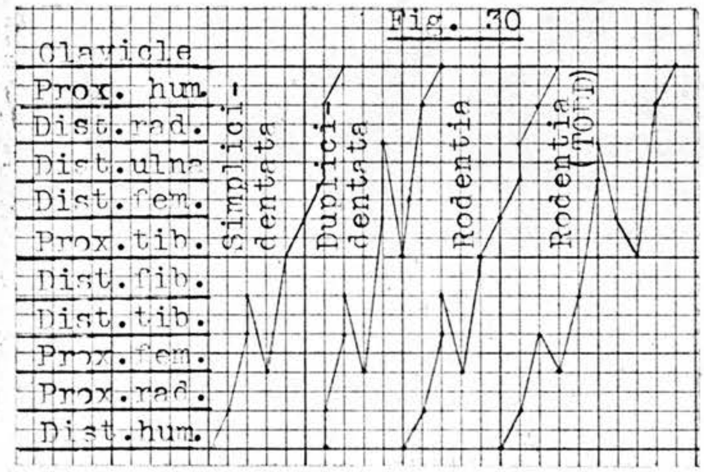

Fig. 30.

Graphs showing on the Stevenson scale the Sequences of Epiphysial Fusion in Simplicidentata and Duplicidentata and the average of Sequences in Rodentia as given in this work (Basu) and by Todd.

Todd[31]	Present work
Fem., head	Tib., prox.
Fem., gr. tr.	Hum., prox.
Fem., dist.	
Fib., prox.	
Hum., prox.	
Tib., prox.	
Rad., dist.	
Ulna, dist.	

Todd had had a large collection of materials to work out the S.E.F. very elaborately in this Sub-order. The present worker, not having the same facility, has to fall in with or arrange his findings in the order given by Todd in the first portion of his table given above. The subsequent arrangement however differs slightly from that of Todd in that the lesser trochanters of femur are given an earlier time of union in Todd's work. Metacarpals, metatarsals and distal radius and ulna, however, are given a later date in Todd's work and therefore differ from Stevenson's schedule. The present work however is in much closer agreement with the latter.

In Fig. 29 is shown the Epiphysial Chart for Duplicidentata. Fig. 30 gives a graphical picture of the average S.E.F. in Simplicidentata, Duplicidentata and Rodentia as a whole. Todd's Average for Rodentia is given for comparison. Stevenson's standard is used.

Reviewing the condition of epiphysial fusion, the following Union Sequence Pattern can be noted for the different groups of Rodentia studied in this work and a sum-total of the result can be drawn up with similar figures given by Todd.

Union Sequence Pattern in Rodentia.

Sciuro-morpha.	Myo-morpha.	Hystrico-morpha.	Average for Simplicidentata.
Pr. & di. el.&di.el. & shaft hum.	Pr.&di.el.& di.el.& shaft hum.,lat.epic. hum	Di.el.hum.	Di.el.hum.
		Pr.el.hum.	Pr.el.hum.
Lat.epic.hum.,pr. rad.&ulna,mcl, phal.(all),calc. ep.	Di. tib.	Di.ep.& shaft *hum.	Di.ep.& shaft hum.
	Pr.rad.	Lat.epic.hum.	Lat.epic.hum.
Mc (outer),mt's.	Calc.ep.	Phal.III(all)	Phal.III(all)
(Med.epic.hum), Fem.,trochs.	Di.fib.	Pr.rad.	Pr.rad.
Fem.,head.	Med.epic.hum.	Ph.I&II(all), calc.ep.,mt's.	Ph.I&II (all), calc. ep.
Di.tib, di.fib.	Fem.,ls.tr.	Mc's.,fem.,ls. tr.,di.tib., di.fib.	Mc's & mt's.
Di. ulna	Fem.,hd.		Med.epic.hum., pr.ulna
Di.rad.,pr.tib., pr.fib.,st.& ac. clav.	Pr.ulna	Med.epic.hum.	
	Fem.,gr.tr.	Pr.ulna	Di.tib. & di.fib.
Di.fem.	Clav.,ac.		Fem.ls.tr.
Pr.hum.	Tib, tb.	Fem.,hd.& ls. tr.	Fem. hd. & gr.tr.
		Di.fem.	
	No further observations	Pr.tib.	Clav. ac.
	*Mc's & Mt's (outer), phal.manus & pes	Di.rad.,di. ulna,pr.hum.	Pr.tib, pr. fib.
		Clav. st.	Di.fem.
			Di.rad., di. ulna, pr.hum.
			Clav. st.

Union Sequence Pattern in Rodentia.

(continued from previous page)

Average for Simplicidenta.

- Di.el.hum.
- Pr.el.hum.
- Di.ep.&shaft hum.
- Lat.epic.hum.
- Phal.III(all)
- Pr.rad.
- Ph.I & II (all), calc.ep.
- Mc's & mt's.
- Med. epic. hum., pr.ulna
- Di.tib. & fib.
- Fem. ls. tr.
- Fem.hd. & gr.tr.
- Clav. ac.
- Pr.tib. & fib.
- Di. fem.
- Di.rad. & ulna, pr. hum.
- Clav. st.

Average for Duplicidentata.

- Pr.el.hum. ,all ep.for di.end hum.,pr.rad., all ep.for manus & pes.
- Pr.ulna,di. tib.(fib.)
- Pr.fem.(all), tib.tb.
- Di.fem.,pr.fib., di.rad. & ulna.
- Tib. cond.
- Pr. hum.

Average for Rodentia.

- Di.el.hum.
- Pr.el.hum.
- Di.ep. & shaft hum.
- Lat. epic. hum.
- Ph.III(all)
- Pr. rad.
- Ph.I &II(all), calc. ep.
- Mc's & mt's.
- Med.epic.hum.
- Pr. ulna
- Di. tib. & fib.
- Fem. ls. tr.
- Fem. hd. & gr. tr.
- Clav. ac.
- Pr. fib.
- Pr. tib.
- Di. fem.
- Di. rad. & ul.
- Pr. hum.
- Clav. st.

Todd's Average for Rodentia.

- Di.ep.& shaft hum.
- Ph. III (all)
- Ph. II(manus)
- Ph. II(pes)
- Med.epic.hum.
- Ph.I (all)
- Pr. rad.
- Calc. ep.
- Fem. ls. tr.
- Mc's.
- Mt's.
- Di. tib.
- Fem. hd.
- Clav. ac.
- Pr. ulna
- Di. fib.
- Fem. gr. tr.
- Di.rad. & ulna
- Pr. fib.
- Di. fem.
- Pr. tib.
- Pr. hum.
- Clav. st.

no wear   no wear

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Table No.45

List of Carnivora (Fissipedia) skeletons studied.

Section, Family, Sub-family, Genus &c.	Number of skeletons Total	Young	Adult	Habits, Special features &c.
AELUROIDEA				
Felidae	36	22	14	Digitigrade: manus, 5- & pes, 4- toed. Claws retractile.
F.domesticus	10	7	3	Can climb trees.
Manx cat	1	1	-	
F.catus	4	4	-	
F.bengalensis	1	1	-	
F.tigris	4	1	3	Can climb trees.
F.Concolor	1	-	1	
F.pardus	4	3	1	
Others	3	-	3	
F.leo	7	5	2	Cannot climb trees.
Cyanaelurus	1	-	1	Long-legged.
Viverridae	11	6	5	Head & body proportionately longer. Specialisation at a lower level than Felidae. Digits usually 5 in each paw
S.F.Euplerinae	1	1	-	
S.F.Cryptoproctinae	1	-	1	
S.F.Viverrinae				
Viverra	2	-	2	
Arcticitis	2	1	1	
Paradoxurus	2	2	-	
Cynogale	1	-	1	Partly aquatic.
S.F.Herpestinae				
Herpestes	1	1	-	Cat-like; 5 toes in each paw.
Suricata	1	1	-	4 toes in each paw.
Hyaenidae	1	-	1	4 toes in each paw. Hind limbs shorter.
CYNOIDEA Canidae	41	8	33	Digitigrade; manus, 4- or 5- & pes, 4- toed. Claws non-retractile.
C.familiaris	29	8	21	Manus, 5 toes; Pollex very short Pes, 4 toes & metatarsal only of hallux.
Others	12	-	12	
ARCTOIDEA				
Ursidae	10	7	3	Plantigrade. 5-dactyle.
Procyonidae	10	1	9	
Aelurus	3	1	2	
Procyon	2	-	2	Longish limb. Very mobile digits.
Others	5	-	5	
Mustelidae	22	5	17	Elongated bodies; usually 5-dactyle. Planti- or digitigrade.
S.F.Lutrinae	3	1	2	Toes webbed, aquatic.
S.F.Melinae	10	1	9	Feet long, terrestrial fossorial.
S.F.Mustelinae	9	3	6	Toes short, partly webbed. Terrestrial & arboreal.
Total.	131	49	82	

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no wear no wear

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Table No. 46

Order: CARNIVORA Sub-order: Fissipedia Sec: Aeluroidea

..am	F e l i d a e						
..us	F e l i s						
..	F.domesticus	F.domesticus	F.domesticus	Manx cat	Cat	Cat	Cat
..sum	W.R.U.	E.U.A.	W.R.U.	E.U.A	E.U.A	R.D.V.C	R.D.V.C.
..ber	B 64	56,XXXVII	B 63	56,XVII a&b	56,III	B.R Male	gal,4
	young	young	young adult				
EPIPHYSES							
..lav, St....) Ac....)	Never present						
..m, Pr.El.	+	+	+	+	+	M	+
" & Sh.	-	-	- to B	B	R	M	R
Di.El.	+	+	+	+	+	M	+
" & Sh.	R	+	+	+	+	M	+
Lat.Ep.	R	+	+	+	+	M	+
Med.Ep.	B	B	+	+	+	M	+
..d, Prox..	-	+	+	+	+	+	+
Dist..	-	-	B	R	R	+	+
..na, Prox..	-	+	+	+	+	+	+
Dist..	-	-	- to B	R	R	R	+
.., First.	M	+	+	+	+	+	+
Rest..	M	+	+	+	+	+	+
..(M), Prox..	M	+	+	+	+	+	+
Mid...	M	+	+	+	+	+	+
Term..	M	+	+	+	+	+	+
..m, Head..	-	B	B	B	+	+	+
Gr.Tr.	-	B	B	B	+	+	+
Ls.Tr.	-	R	B	R	+	+	+
Dist..	-	B	B	B	R	+	+
..b, Con...	-	B	B	B	R	+	R
Tb....	-	R	B	B	+	+	R
Dist..	-	R	+	+	+	+	+
..b, Prox..	M	-	B	R	+	+	+
Dist..	M	R	+	+	+	+	+
..lc. Epip..	M	+	+	+	+	+	+
.., First.	absent						
Rest..	M	+	+	+	+	+	+
..(P), Prox..	M	+	+	+	+	+	+
Mid...	M	+	+	+	+	+	+
Term..	M	+	+	+	+	+	+
..t.Centre..							
..L.FEATURE.							
..BITS ETC..	Digitigrade						
..MARKS.....							
..ITION...	Standard						
	no wear		no wear				

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Table No. 47

Order: CARNIVORA Sub-order: Fissipedia Sec: Aeluroidea

F e l i d a e

F e l i s

F. domesticus	F. bengalensis	F. catus	F. catus	Scottish Wild cat	Wild cat
E.U.Z. B.C.	I.M. M.gal, 21	R.S. 1884, 54.2	E.U.Z. P.P. 1.1	R.D.V.C. B.R.	E.U.A. 56, I
nil	nil	nil	nil or gl. nil	nil	nil
+	+	+	+	+	+
R	-	-	B	B+	+
+	+	+	+	+	+
+	+	+	+	+	+
+	+	+	+	+	+
+	R	+	+	+	+
+	+	+	+	+	+
+	-	-	R	R	+
+	B	R	+	+	+
+	-	-	B+	R	+
+	?	+	+	+	+
+	?	R	+	+	+
+	?	+	+	+	+
+	?	+	+	+	+
M	?	+	+	+	+
+	-	B	R	+	+
+	-	-	+	+	+
+	-	-	+	+	+
+	-	-	+	R	R
+	-	-	R	R	+
+	-	-	R	R	+
+	-	-	+	+	+
+	-	-	R	+	+
+	-	-	+	+	+
+	+	+	+	+	+
		absent			
+	?	+	+	+	+
+	?	+	+	+	+
+	?	+	+	+	+
+	?	+	+	+	+
Standard	M_1 crypt / M_1 erupted P_3 not in dm $\frac{1}{0}$ still in	$\frac{3.1.2.1}{3\ 1\ 3\ 1}$	Standard	$\frac{3.1.4.1}{3\ 1\ 3\ 2}$	$\frac{3.1.2.1}{3\ 1\ 2\ 1}$

Table No. 48

Order: CARNIVORA Sub-Order: Fissipedia Sec: Aeluroidea

Felidae

Felis

F.leo	F.leo	F.leo	Mountain Lion	F.leo	F.pardus	Tiger	F.pardus	F.pardus
WRU	W.R.U	W.R.U	W.R.U	E.U.A	R.S.	I.M.	E.U.A.	E.U.A.
B73	B72	B334	F.E.R's	56XXIII	C20	SM,m.g.	56XIV-XVIb	56XXIV
		Fem.						
young	young	Y.adult 1½ yrs	y.adult					
M	x	x	x	x	x	x	x	x
M	x	x	x	x	x	x	x	x
+	M	+	+	+	+	+	+	+
-	M	-	B	B	-	-	-	R
+	M	+	+	+	+	+	+	+
-	M	+	+	+	+	+	+	+
-	M	R	+	+	+	+	+	+
-	M	+	+	+	+	+	+	+
-	M	B	D	+	+	+	M	+
-	M	-	B	R	-	-	M	+
-	M	-	B	+	B	+	M	+
-	M	-	B	R	-	B	M	+
-	M	+	+	+	+	+	M	+
-	M	+	B	+	+	+	M	+
- to B	M	+	+	+	+	+	M	+
do.	M	+	+	+	+	+	M	+
+	M	+	M	+ or nil	+	+	M	+
-	-	-	B	R	-	B +	B	+
-	-	-	B	+	-	R	R	+
nil	-	-	ct.?	+	B	R	+	+
-	-	-	B	B	-	B	-	+
-	-	-	B	B	-	B	-	+
-	-	-	B	R	-	-	-	+
-	- to B	B	B	+	R	+	+	+
-	-	-	B	R	-	-	M	+
-	B	-	B	+	B	R	M	+
-	- to B	+	B	+	+	+	M	+
-	B	+	v e s t i g i a l					
-	B	+	B	+	+	+	M	+
to B	B	+	+	+	+	+	M	+
-	B	+	+	+	+	+	M	+
+	+	+	M	+	+	+	M	+

teoan
ar phalax

skull	no skull	zoo sp.	no skull			artic.skel.	fragmentary	Styloid ulna artic. with ulnare
	skel. fragmentary	badly malnourished. Teeth much decayed						
		some I cutting, some cut Baby canines worn per. can. impacted.		$\frac{3.1.2.1}{3\ 1\ 2\ 1}$	$\frac{3.1.2.1}{3\ 1\ 2\ 1}$	$\frac{3.1.2.1}{3\ 1\ 2\ 1}$ no wear	M	$\frac{3.\ 1.\ 2.\ 1}{3\ \ 1\ \ 2\ \ 1}$

THE STUDY OF EPIPHYSIS IN CARNIVORA (FISSIPEDIA).

This order consists of small to large quadrupeds ; terrestrial, arboreal or aquatic ; usually carnivorous ; 3 incisors on each side in each jaw, projecting canines, last upper molar and first true lower molar always "carnassial" or "sectorial" ; clavicles incomplete or absent; scaphoid and lunate fused ; toes never less than four, armed usually with strong and sharp claws and cleft ; ulna and fibula distinct ; no third trochanter in femur ; pollex and hallux not opposable ; animals digitigrade or semi-digitigrade (bears are plantigrade).

The living Carnivora may be classified in three sections, the cat-like or "Aeluroidea", the dog-like or "Cynoidea" and the bear-like or "Arctoidea".

Section: AELUROIDEA.

Family: FELIDAE. digitigrade animals ; manus has 5 and pes 4 digits ; claws retractile.

36 skeletons were available for study ; 22 of these were young and have been listed in Tables No. 46, 47 & 48. The remaining 14 were of adult animals. These are shown below:-

F. domesticus	- 3	(WRU, B1127 & B2154 ; & RDVC, BR)
F. leo	- 2	(WRU, B173f ; & RS, C21)
F. tigris	- 3	(WRU, B611f ; IM, m.g,C7m;& RS,C4&C5)
F. concolor	- 1	(WRU, B839m)
F. pardus	- 1	(IM, s.m.g, comparative, fore-limb only
F. nebulosa	- 1	(IM, m.g, C20)
F. serval	- 1	(RS, 1873.18)
F. chaus	- 1	(IM, m.g, C22)
Cynaelurus jubata	- 1	(IM, m.g,f)

1. Felis domesticus: 8 young specimens (including a manx cat) showed the S.E.F. as follows (Tables No. 46 & 47) :-

In Skel.	WRU, B64	... ep.	3,5 (manus & pes M)
" "	EUA, 56XXXVII further	... "	6,7,9,11,13 to 17, 27 to 32
" "	WRU, B63 & EUA, 56XVII,a&b) "	... "	8, 24, 26
" "	" 56III "	... "	18, 19, 20, 23, 25
" "	RDVC, BR "	... "	10, 21, 22
" "	" Gall,C4 "	... "	12(but 22&23 in'R'stage)
" "	EUZ, B.C. "	... "	12,22,23 (4 is 'R')
" "	of adults presumably "	... "	4

2. Felis catus: 4 young specimens examined (Table No.47).

Their S.E.F. along with the E.F. in 1 specimen of F. bengalensis is given below:-

In Skel.	IM,m.g,C21	... ep.	3,5,6,7,9,37 (manus & pes handicapped)
" "	RS,1884,54.2 further	... "	8,13,15,16,17,27 to 32 (11 is 'R')
" "	EUZ,PP1.1 "	... "	11,14,18,19,20,21,24,26
" "	RDVC,BR "	... "	25 (21 is 'R')
" "	EUA,56I "	... "	4,10,12,22,23(21 is 'R')

Note that ep.21 (distal femur) may be the last to fuse.

3. Felis leo: of 7 specimens examined, 5 were from young animals and showed the following S.E.F.(Table No.48):-

In Skel.	WRU,B73 & B72	... ep.	3,5,17,32
" "	" F.F.R's further	... "	6,7,8,13,15,16,30,31
" "	" B334f "	... "	14,27,29 (7 is 'R')
" "	EUA,56XXIII "	... "	9,11,19,20,24,26

4. Felis tigris: Of 4 skeletons examined, only 1 was of a young animal.

5. Felis pardus: Of 4 skeletons studied, 3 were young.

The S.E.F. in the 4 skeletons (1 of tiger & 3 of leopards - Table No.48) is shown together as below:-

ierate wear Upper & lower dc & dm in lower P_2 crypt 3 1 4 2 no wear 3 1 3 2 slight wear

In Skel. RS,C20 ... ep. 3,5,to 9,13 to17,27 to 32
" " IM,s.m.g further ... " 11,24
" " EUA,56XIV to XVIb " ... " 20
" " " 56XXIV " ... " 10,12,18,19,21,22,23,25,26
" " of adults presumably further ep. 4

Sorting out the S.E.F's in F. domesticus, catus, leo, tigris and pardus, the following is obtained:-

In F.domesticus,WRU,B64 fusion of ep. 3,5
" F.leo " B72&B73 " " " 3,5,17,32
" " " F.E.R's " " " 3,5,6,7,8,13,15,16,17 30,31,32
" F.bengalensis, IM,m.g,C21 " " " 3,5,6,7,9,27 (8 is 'R')

Note that the manus and pes in this specimen were handicapped. Presumably they had at least the same fusion as in the next skeleton of its relative, F.catus, RS,1884,54.2.

In F.catus,RS,1884,54.2 fusion of ep. 3,5,6,7,8,9,13,15,16, 17,27,29,30,31,32
" F.leo, WRU,B334f " " " 3,5 to 8,13 to 17,27, 29 to 32 (7 is 'R' & 9 is 'B')
" F.pardus,RS,C20 " " " 3,5,9,13 to 17,27 to 32
" F.domesticus,EUA,56XXXVII " " " 3,5 to 9,11,13 to 17, 27 to 32 (8 is 'B')
" F.tigris,IM,s.m.g. " " " 3,5 to 9,11,13 to 17, 24, 27 to 32
" F.pardus,EUA,56XIV to XVIb " " " 3,5 to 8,20,24(radius, ulna,manus & pes M)
" F.domesticus,WRU,B63 & EUA,56XVII,a & b) " " " 3,5 to 9,11,13 to 17, 24,26,27 to 32 (20 is 'B' in WRU,B63 & 'R' in the other)
" F,leo,EUA,56XXIII " " " 3,5 to 9,11,13 to 17, 19,20,24,26
" F.catus,RDVC,BR " " " same as above & 18,25
" F.domesticus, EUA,56III " " " " " " & 23
" F.catus,EUZ,PP1.1 " " " " " " & 21
" F.domesticus,RDVC,BR " " " " " " & 10,22
" " " Gal 4 " " " " " " & 12
(22 & 23 are 'R')
" " EUZ,BC &) " " " 3,5 to 8,9 to 12,13 to
" F.pardus,EUA,56XXIV) 17,18 to 21, 22 to 24, 25, 26, 27 to 32
" F. catus,EUA,56I further " " " 4(but 21 is 'R')

derate wear Upper & lower dc & dm in lower P_2 crypt 3 1 3 2 3 1 4 2 no wear 3 1 3 2 slight wear

In adult skeletons of F. tigris, pardus & domesticus, ep. 4 is presumably the last.

From the above, it will be seen that ep. 8 is accelerated in lions, but retarded in cats; and ep. 9 is retarded in lions but accelerated in cats, leopards and tigers; i.e., in climbers proximal radius unites earlier than in non-climbers, but in the latter medial epicondyle of humerus unites earlier than in the former.

The sequence of Epiphysial Fusion in Felidae is therefore as follows:-

Proximal & distal elements humerus
Terminal phalanges
Distal epiphysis & lateral condyle with shaft humerus; 1st metacarpal ; middle & proximal phalanges.
Proximal radius; calcaneal epiphysis.
Medial epicondyle humerus; metatarsals.
Metacarpals.
Proximal ulna.
Distal tibia.
Lesser trochanter femur.
Distal fibula.
Greater trochanter femur.
Head femur; proximal fibula.
Tubercle of tibia.
Distal femur.
Proximal tibia; distal radius.
Distal ulna.
Proximal humerus.

<u>Family VIVERRIDAE:</u> Small animals with longer bodies and heads and specialization at a lower level than Felidae: planti - or digiti-grade; manus and pes usually with 5 digits (pollex or hallux may be absent).

Table No. 49

Order: CARNIVORA Sub-Order: Fissipedia Sec: Aeluroidea

	Viverridae					
	Arcticitis	Paradoxurus		Herpestis	Eupleres	Surichata
	A. binturong	P. hermaphroditus	P. hermaphroditus	H. punctatissimus	E. goudoti	S. tetradactyla
m r	I.M. m.gal, 25 Male	I.M, m.g. 10983 Male young	R.S. C20	W.R.U. B 612 y. adult	R.S. 1886, 16.7	W.R.U. B 613
	nil	nil	nil	nil	nil	nil
	+	+	+	+	+	+
	-	-	R	-	B	+
	+	+	+	+	+	+
	B+	+	+	+	+	+
	R	+	+	+	+	+
	B	+	+	+	+	+
	-	B	+	+	+	+
	-	-	+	-	+	+
	B	R	+	B	+	+
	-	-	+	-	+	+
	-	B	+	+	+	vest
	-	B	+	+	+	+
	B	+	+	+	+	+
	R	+	+	+	+	+
	+	+	+	+	+	+
	-	-	+	B	R	+
	-	B	+	B	R	+
	-	- or nil	+	B	+	+
	-	-	+	B	R	R
	-	-	+	B	R	R
	-	-	+	B	B	R
	-	B	+	B+	+	+
	-	-	+	-	+	+
	-	B	+	B+	+	+
	-	+	+	+	+	+
	-	vest	vest	vest	+	vest
	-	B	+	+	+	+
	- to B	+	+	+	+	+
	+	+	+	+	+	+
	+	+	+	+	+	+
	rtic. skel.	Artic. & ligamentous sk.				ligamentous spec.
	3.1.3.2 3 1 3 2 derate wear	3.1.2.2 3 0 1 2 Upper & lower dc & dm in lower P_2 crypt	3.1.4.2 3 1 3 2	3.1.4.2 3 1 4 2 no wear		3.1.3.2 3 1 3 2 slight wear

Of 11 specimens examined, 5 were adults as follows:-

Arcticitis binturong,	WRU, B245m
Cryptoprocta ferox,	WRU, B244m
Viverra zibetha,	IM, m.g, C24
Viverra malacensis,	WRU, B245, gallery
Cynogale bennetti,	IM, m.g, C25m

In the remaining 6 specimens, the S.E.F., irrespective of the species is as follows:- (vide Table No.49)

In Skel.	IM,m.g,C25m		fusion of ep.	3,5,17,31,32
" "	" 10983m	further	" " "	6,7,8,15,16,27,30
" "	WRU,B612	"	" " "	9,13,14,29
" "	RS,1896,16.7	"	" " "	10,11,12,20,24,25,26
" "	WRU,B613	"	" " "	(4?),18,19(21,22,23'R')
" "	RS,C20	"	" " "	21,22,23 (4 'R')
" " of adults presumably further fusion of ep. 4				

Hence the sequence of Ep. fusion in Viverridae is as follows:-

Proximal & distal elements humerus; terminal & middle phalanges pes; terminal phalanx manus.
Distal epiphysis & epicondyles with shaft humerus; proximal & middle phalanges manus; calcaneal ep; proximal phalanx pes.
Proximal radius; metatarsals; metacarpals.
Proximal ulna; distal tibia & fibula; lesser trochanter femur; proximal fibula; distal radius; distal ulna.
Head femur; greater trochanter femur; proximal humerus?
Distal femur; proximal tibia.
Proximal humerus.

<u>Family HYAENIDAE:</u> Only one fully adult specimen was available.

A review of the S.E.F. in Aeluroidea shows that the proximal femoral epiphyses are very much retarded and the proximal tibia is retarded to a lesser degree. This is a characteristic feature of Aeluroidea. In Viverridae, it will be seen that the head and greater trochanter of femur are even

3 1 3 3 No wear No wear 3 1 3 2 Lower P_1 absent 3 1 4 2

Table No. 50

Order: CARNIVORA Sub-order: Fissipedia Sec: Cynoidea

C a n i d a e

C a n i s

	C. fami-liaris (Borzoi)	C. famil. (Russian wolf-hound)	C. famil. (Airdale)	C. famil. (Boston bull)	C. famil. (Whippet)	C. famil.	C. famil. (Bull dog)	C. famil. (Scottish Deer-hound)
m	E.U.A.	W.R.U.	W.R.U.	W.R.U.	E.U.A.	R.S.	E.U.Z.	E.U.A.
r	J.C.B's	B2096	B835	B96	56, IV	C, 22	E.C, V5	56, XI
		Fem.	Fem.	Male				Male
		abt. 6 mths.	10 mths.	13mths				4 years
	?	?	?	?	?	?	?	?
	+	+	+	+	+	+	+	+
	-	-	B	B	R	R	R	+
	+	+	+	+	+	+	+	+
	B	+	+	+	+	+	+	+
	-	+	+	+	+	+	+	+
	-	+	+	+	+	+	+	+
	-	B	+	+	+	+	+	+
	-	-	R	+	+	+	+	+
	B	B	+	+	+	+	+	+
	-	-	+	+	+	+	+	+
	x	x	+	+	+	+	+	+
	-	B?	‡	+	+	+	+	+
	R	B?	+	+	+	+	+	+
	R	B?	+	+	+	+	+	+
	+	+?	+	+	+	+	+	+
	-	B	+	+	+	+	+	+
	-	B	B+	+	+	+	+	+
	-	B	B+	+	+	+	+	+
	-	B	B+	+	+	+	+	+
	-	B	B	+	R	+	+	+
	-	B	B	B	+	+	+	R
	-	B	B+	+	+	+	+	+
	-	-	-	B+	+	+	+	+
	-	B	B	+	+	+	+	+
	R	B?	+	+	+	+	+	+
				absent				
	-	B?	+	+	+	+	+	+
	R	B?	+	+	+	+	+	+
	R	B?	+	+	+	+	+	+
	+	+?	+	+	+	+	+	+
	culiar hollow one-like ep. at stal ulna							
		Manus & Pes unmacerated	poor calci-fication. Genl. growth erratic					
	3.1.3.2 / 3 1 3 3	Good & comp. No wear	Stand. No wear	3.1.4.2 / 3 1 3 2 Lower P_1 absent	Stand.	Stand.	Stand.	3.1.4.3 / 3 1 4 2

more retarded; so is also the proximal tibia. It may be argued that this feature is characteristic of animals with tremendous power of leaping on the ground and with a highly agile body. Scansorial powers are associated with an early fusion of proximal radius and, in long-leaping animals devoid of climbing ability, the medial epicondyle is accelerated.

Section CYNOIDEA:

Family CANIDAE: Digitigrade ; manus has four or five digits, pes has four.

Canis: Clavicles reduced ; manus has five digits, pollex is very short; pe has four outer toes, the metacarpal only of the first toe being present.

40 specimens were examined. 8 of these are listed in Table No.50. The remaining 32 adult skeletons for study were as follows:-

Boston Bull-dog	- WRU,B2158,m
Canis familiaries	- FUZ,BC,V,1; EUZ 24 EUA,56V; 56VI; and 56XII RDVC,C4 WRU,B110,m; B2099,m; B2100; B2155,m
Collie (Scotch	- WRU, B128,m; B224
German Police Dog (thoroughbred)	- WRU, B1143,m
Mastiff	- WRU, B111,m
Newfoundland	- WRU, B645,m
St. Bernard (purebred)	- WRU, B403
Terrier	- WRU, B2153,f
Bull Terrier	- RDVC, BR
Fox Terrier	- WRU, B2159,f
Indian Wild Dog	- RS, C22
Dingo	- RDVC, BR; EUZ, PP24.1
Wolf	- EUA, 56VII
Timber Wolf	- EUZ, BC, V,4 (1939-11)
Canis aureus	- IM, C28

or P_2& M_3not out $P \frac{}{1}$ absent out

m_1 still in
M_2 not in
M_2 & M_3 not in

Canis vulpes	-	EUA, 56XIII; EUZ, PP28.1
Fox	-	EUA, 56II
Silver Fox	-	EUZ, BC,VII, 2,m
Vulpes vulgaris	-	WRU, B1316
Vulpes vulpes	-	RS, C22

The S.E.F. in the young skeletons as seen from Table No.50 is as follows:-

In Skel. of Borzoi (EUA, J.C.B's) fusion of ep. 3,5,17,32
" " WRU, B2098,f further " " " 6,7,8
" " WRU, B835,f " " " " 9,11,12,13 to 16,18,27 to 31
" " WRU, B96,m " " " " 10,19,20,21,22, 24,26
" " EUA, 56IV) RS, C22 &) EUZ, BC,V,5) " " " " 23,25(22 is 'R' in EUA, 56IV)
" " EUA, 56XI,m " " " " 4 (23 is 'R')

The S.E.F. in Cynoidea so far as could be gathered from the present study can be represented as follows:-

Proximal & distal elements humerus ; terminal phalanges
Distal epiphysis & epicondyles with shaft humerus.
Middle & terminal phalanges; metacarpals ; metatarsals; calcaneal epiphysis; proximal radius; proximal ulna; head femur; distal ulna.
Femoral trochanters; distal tibia & fibula; distal femur; proximal tibia; distal radius.
Tubercle tibia; proximal fibula.
Proximal humerus.

Compared with the S.E.F. in Aeluroidea(Felidae), that in Cynoidea shows that distal ulna is accelerated out of proportion to all other epiphyses corresponding to the second spurt of fusion in generalised mammals. The retardation affects proximal fibula only.

wer P_2& M_3not out $m_1$still in $P \frac{1}{1}$ absent M_3 not out, lower M_3 not out
M_2 not in
M_2 & M_3 not in

Table No. 51

Order: CARNIVORA Sub-order: Fissipedia Sec: Arctoidea

U r s i d a e					
U r s u s					Helarctus
U.americanus	U.malayanus	U.arctos	U.americanus	U.americanus	Helarctus malayanus
W.R.U.	W.R.U.	R.S.	W.R.U.	W.R.U.	E.U.A.
B 836	B 635	C.25	B 635	B 636	56, XXXVI
Male	Male		Male	Female	
16 hum.yrs.					
nil	nil	nil	nil	nil	nil
+	+	+	+	+	+
-	-	-	-	B	+
+	+	+	+	+	+
+	+	+	+	+	+
+	R	+	+	+	+
B	B	+	R	R	+
+	+	+	+	+	+
-	-	-	-	-	+
-	B	R	B	B	+
-	-	-	-	-	+
+	+	+	+	+	+
+	+	+	+	+	+
+	+	+	+	+	+
+	+	+	+	+	+
+	+	+	+	+	+
-	B	B	-	B	+
-	B	B	B	B	+
B	B	B	B+	+	+
-	-	-	-	B	+
-	-	-	-	B	R
-	-	-	-	B	+
-	-	B	R	R	+
-	-	-	-	-	+
-	-	+	R	B+	+
+	B	R	+	+	+
+	+	+	+	+	+
+	+	+	+	+	+
+	+	+	+	+	+
+	+	+	+	+	+
+	+	+	+	+	+
...h 8 unitos troch. & ...rt hum.					
...tive, zoo spec. ...or nutrition, ...nes deformed.	deformity lt. fem., osteoporosis lt. humerus.			zoo spec., bones in poor state of nutrition and calcification and distorted.	
3.1.4.2 / 3 1 3 2	3.1.3.1 / 3 1 3 1	3.1.3.2 / 3 1 3 3	3.1.4.2 / 3 1 3 2	3.1.4.2 / 3 1 3 2	3.1.3. ? / 3 1 3
P_2 & M_3 not out	dm_1 still in; M_2 not in; M_2 & M_3 not in	P $\frac{1}{1}$ absent	(M_3 not out)	lower M_3 not out	

Section ARCTOIDEA: Plantigrade, pentadactyle.

Family URSIDAE:

9 skeletons were available for examination. 3 of these were adults, viz: Ursus americanus, WRU, B129; Ursus maritimus, WRU, F.E.Randall's collection and IM, m.g, C32,f. The remaining 6 young specimens are listed in Table No.51. Their S.E.F. is:-

In Skel. WRU,B619	fusion of ep.	3,5,6,9,13 to 17, 28 to 32
" " " B836,m) further " B635,m)	" " "	7, 27
" " " B636,f "	" " "	20
" " " RS, C25 "	" " "	8,26 (20 is 'B' & 27 is 'R')
" " " EUA, 56XXXVI "	" " "	4,10,11,12,18,19,21, 23,24,25 (22 is 'R')
" adult skeletons "	" " "	22

i.e. 1) Proximal & distal elements humerus, distal epiphyses with shaft humerus; proximal radius; phalanges; metacarpals; metatarsals.
2) Lateral epicondyle humerus; calcaneal epiphysis.
3) Lesser trochanter femur.
4) Medial epicondyle humerus; distal fibula.
5) Proximal ulna; distal tibia; head and greater trochanter femur; distal radius, ulna & femur; tubercle tibia; proximal fibula; proximal humerus.
6) Proximal tibia.

The above again shows retardation of head femur and epicondyles humerus and proximal ulna. Proximal tibia has been ratarded and proximal humerus precedes it in respect of fusion.

Table No. 52

Order: CARNIVORA Sub-order: Fissipedia Sec: Arctoidea

Procyonidae	M u s	t e l	i d a e		
	Melinae	Mustelinae			Lutrinae
Aelurus	Mydaus	Mustelus	Galictis		Lutra
A.fulgens	Mydaus meliceps	M.putorius	G.barbara	G.vittata	L.vulgaris
W.R.U. B 812.	I.M. m.gal,29	I.M. m.gal,28	W.R.U. B 616	W.R.U. B 646	E.U.A. 56,IX
	v.young		y.adult	nearly adult	
Nil	Nil	Nil	Nil	Nil	Nil
+	+	+	+	+	+
B+	-	-	B-	- - to B	B
+	+	+	+	+	+
+	-	+	+	+	+
+	-	+	+	+	+
+	-	+	+	+	+
+	-	+	+	+	+
+	-	-	- to B	-	B
+	-	+	+	+	+
+	-	-	-	-	B
+	-	?	Rud	Rud	+
+	-	?	R	+	+
+	-	?	+	+	+
+	-	?	+	+	+
+	+	?	+	+	+
+	-	-	- to B	B	B
+	-	B	B	B+	B
+	-	-	+	R+	R
R	-	-	B	B	B
R	-	-	B-	-	B
R	-	-	B-	-	B
+	-	-	B-	B	+
+	-	-	-	-	B
+	-	-	B	B+	+
+	-	?	+	+	+
+	-	?	Rud	Rud	+
+	-	?	R	+	+
+	-	?	+	+	+
+	-	?	+	+	+
+	+	?	+	+	+
	hum. curved like a bow				
	artic. skel.	artic. & ligamentous spec. (manus & pes unmacerated)			
3.1.3.2 / 3 1 4 2	3.1.3.1 / 3 1 3 1	3.1.3.1 / 3 1 3 1	complete except lt. P_1, not appeared.	3.1.3.1 / 3 1 3 2	x
no wear	perm. C & P's just cutting M_2 not in	last M & P_1 not in			

Family PROCYONIDAE:

Procyon has longish limbs, manus handy and great mobility of digits.

Of 10 specimens, only one (see Table No.52) could provide an epiphysial study in the limbs. The remaining 9 specimens were -

Aelurus fulgens, WRU, B254 & IM, m.g, C31
Procyon lotor, EUZ, gal. & EUA, 56, XVIII
Bassariscus astutus, WRU, B256
Nasua narica, WRU, B253
N. olivacea, RS, C23
Cercoleptes caudivolvulus, RS, C23 & WRU, B255

A. fulgens, WRU, B812 showed fusion of ep. 3,5 to 20, 24 to 32.

Taking fusion up to stage (4) of Ursidae, stages (5) and (6) of the latter may be split up into:-

11,24,18,19,10,12 & 25,	i.e.	proximal ulna; distal tibia; head and greater trochanter femur; distal radius and ulna; proximal fibula.
21, 22, 23	i.e.	distal femur; proximal tibia (in 'R' stage in A. fulgens, WRU, B812)
and 4	i.e.	proximal humerus (in 'B ' stage in the above).

Family MUSTELIDAE: Elongated bodies; usually pentadactyle, plantigrade or digitigrade.

Sub-Family Lutrinae: Aquatic; toes webbed.

2 adult specimens (Lutra lutra, RS, C23 & Lutra nair, IM, m.g, C31, f) and 1 young (Table No.52) were examined. The latter showed fusion of epiphyses 3,5 to 9, 11, 13 to 17, 24, 26, 27 to 32.

Ep. 20 being in 'R' stage would fuse next.

Ep: 4, 10, 12, 18, 19, 21, 22, 23 & 25 are all in 'B' stage and no sequence in them can be established from this study. It, however, forms a step between stages (4) and (5) of Ursidae e.g ep. 11, 24. After this may be fitted the stage observed in Procyonidae, viz: ep. 18, 19, 10, 12 & 25.

<u>Sub-Family Mustelinae:</u> Toes short, partly webbed; terrestrial and arboreal.

Of 9 specimens, the epiphyses of 3 (Table No.52) presented material for study. Mustela martes, EUA, 56XIX was a ligamentous preparation; its epiphyses could not be studied. The remaining 5 were adults and are shown below:-

M. martes, RS, 1904, 138,f; WRU, B614; & EUZ, PP39
M. erminea stabilis, RS, 1938, 17
Gulo luscus, RS, C23

In Skel.	IM, m.g, C28		is seen fusion of ep.	3,5 to 9, 11 (13 to 17 & 27 to 32 ligamentous)
" "	WRU, B616	further	" " "	14 to 17,20, 27, 30, 31, 32 (13 & 28 rudimentary)
" " "	B646	"	" " "	29

i.e. the S.E.F. can be put as follows:-

proximal & distal elements humerus; distal epiphyses & epicondyles with shaft humerus; proximal radius; proximal ulna.

phalanges; calcaneal epiphysis; metacarpals; lesser trochanter femur.

metatarsals.

The above is similar to stage 4 of Ursidae minus distal fibula, but with the addition of proximal ulna. It also corresponds to the fusion as seen in Lutrinae less distal tibia and fibula but with lesser trochanter united earlier in Mustelinae.

Sub-Family Melinae: Feet elongated, terrestrial, fossorial.

Only 1 specimen (see Table No.52) was good for epiphysis study, the remaining 9 were adultsas follows:-

Arctonyx collaris,	IM, m.g. C30, m
Meles taxus,	IM, m.g, C30; EUA, 56VIII & 56X
M. meles,	RS, C23
Meles sp.	EUZ, BC, V,3
Mellivora indicis,	IM, m.g, C30,m
Helictis nipalensis,	IM, m.g, C29
Ictonyx lybica,	WRU, B615

Mydaus meliceps, IM, m.g, C29 showed fusion of ep. 3,17,32.

The S.E.F. in Mustelidae may therefore be arranged as follows:-

1.	3,17,32	i.e.	proximal elements humerus; terminal phalanges.
2.	5 to 9,11,13 to 17, 27 to 32	"	distal elements humerus; prox.radius; prox.ulna; distal epiphysis and epicondyles with shaft humerus; calcaneal epiphysis; phalanges; metacarpals, metatarsals.
3.	20	"	lesser trochanter femur.
4.	24, 26	"	distal tibia & fibula.

There was not enough Mustelidae material to study fusion of epiphysis beyond this stage.

On comparison with Ursidae, it is seen that fusion of proximal ulna, epicondyles of humerus and calcaneal epiphysis may be separated from stage (2) and distal tibia from stage (4) in the S.E.F for Mustelidae as given above and, by comparison with the sequence in Ursidae and Procyonidae, the S.E.F for Arctoidea may be written thus:-

3, 17, 32	i.e.	prox. elem. hum.; terminal phalanges.
5,6,9,13 to 16, 28 to 32	"	dist. elem. & ep. hum.; prox. rad.; metacarps. & metatars.; prox.& mid. phal.
7, 27, 9	"	lat. & med. epic. humerus; calcaneal ep.
11, 20	"	prox. ulna; lesser trochanter femur.
26	"	distal fibula.
24	"	distal tibia.
18,19,10,12,25	"	head and greater trochanter femur; dist. radius & ulna; prox. fibula.
4?	"	proximal humerus?
21,23,22?,4?	"	dist. fem.; tub., cond.?, tib; prox. hum?
22 (Ursidae) 4 (Procyonidae)	"	Condyle tibia;proximal humerus.

DISCUSSION:

On reviewing the habits of animals comprising the Fissipedia, it is seen that the Order consists of very fast moving land animals with marked leaping, running and often climbing powers. Their limbs are usually short in proportion

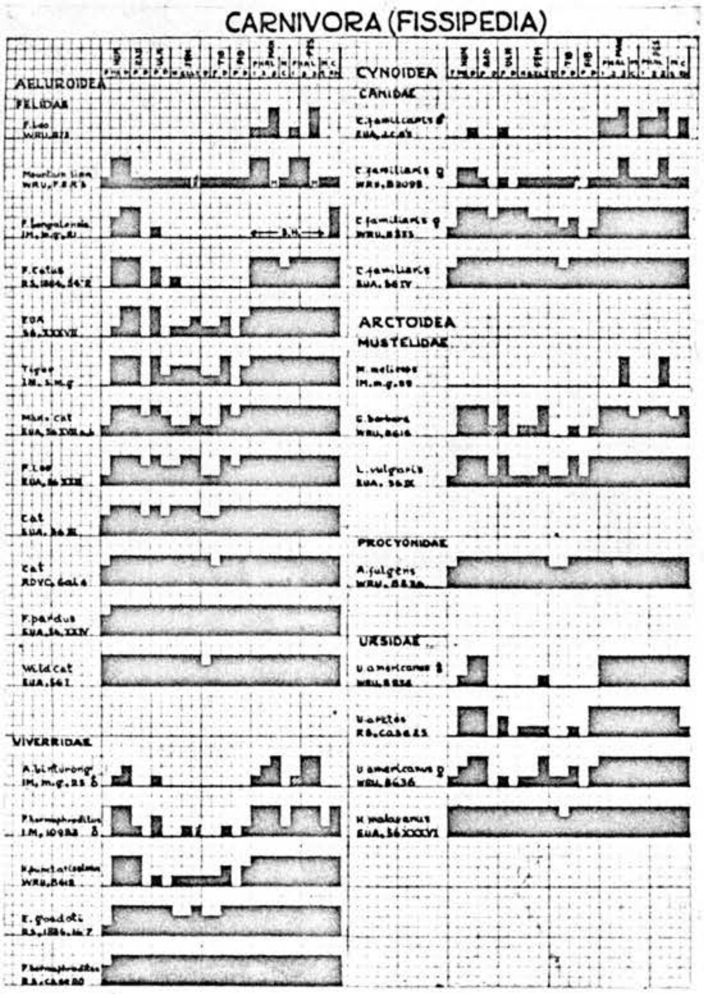


Fig. 71.
Epiphysial Chart
for
Fissipedia

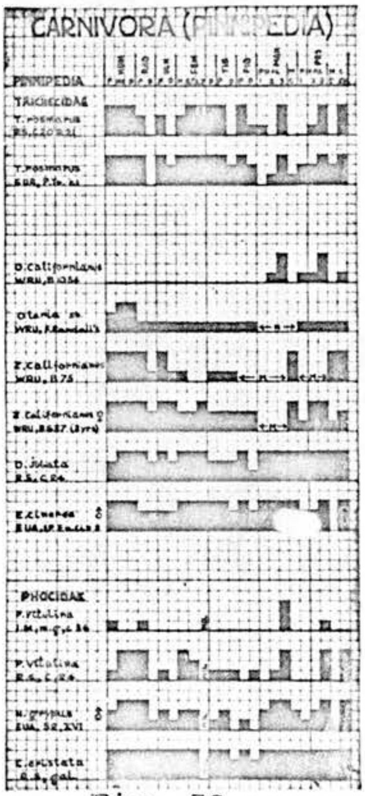


Fig. 32.
Epiphysial Chart
for
Pinnipedia

Abbreviations.- M, missing; G, 'glazing'; S.H., study handicapped; Nil, no epiphysial centre. Hatching indicates different epiphysial stage on two sides or in members of the same series.

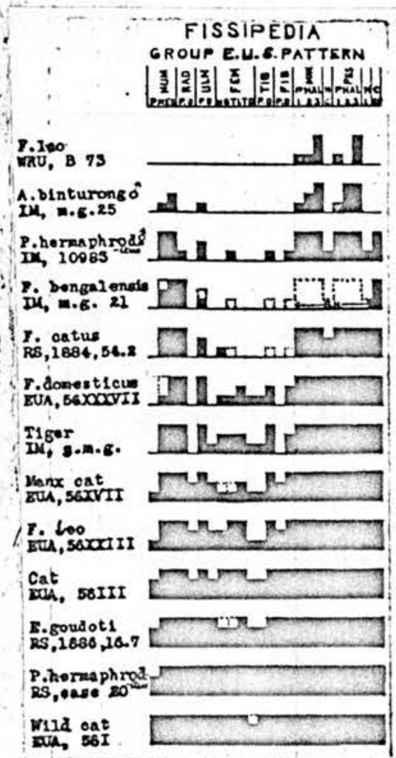


Fig. 33.
Group-pattern of E.U.S. of Fissipedia.

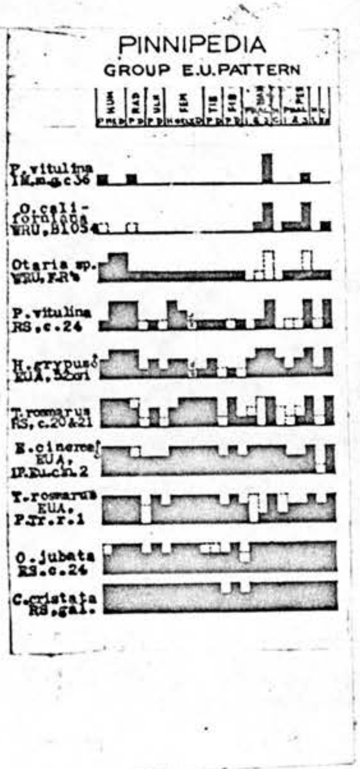


Fig. 34.
Group-pattern of E.U.S. of Pinnipedia.

Nil stands for absence of epiphysial centre. Dotted lines round clear space indicate a probability in epiphysial condition that has not materialised. Hatching, as explained before.

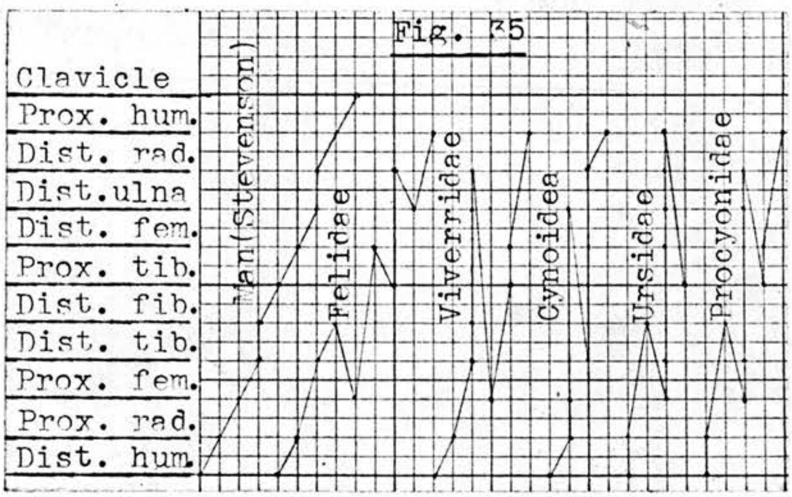


Fig. 35.

Graphs showing the Sequences of Epiphysial Fusion in the different Sections and Families of Carnivora (Fissipedia) as compared with Man (Stevenson).

to the body and on account of the great leaping powers entrusted on them the wrist and ankle have to bear the brunt of the strain. Epiphyses at any one end or at both ends of these joints must necessarily fuse earlier than the schedule for animals studied before.

In section Aeluroidea, distal tibia and distal fibula (ankle) fuse earlier than head femur in Felidae. These are further joined by distal radius and distal ulna (wrist) in Viverridae, which consists of smaller animals with greater scansorial powers.

In section Arctoidea, though heavy bodied and comparatively sluggish, yet Ursidae shows earlier fusion of distal fibula and tibia than head femur. Its proximal tibia, however, remains unfused till the last. The distal radius and ulna fuse earlier than distal femur and proximal tibia in Procyonidae (p.136) and probably also in Lutrinae (Mustelidae).

Cynoidea comprises swift animals with very limited scansorial ability. In it distal ulna is visibly accelerated, followed perhaps by distal radius and femur and proximal tibia, i.e., hip, wrist and knee are consolidated earlier than ankle.

Thus the characteristic features in the long leaping Fissipedia, are the modifications of the fusion of epiphyses in the first phase, which excludes head femur (hip) from it (except in Cynoidea) and may include distal radius or ulna or both (wrist) within it. Proximal tibia and fibula may therefore compete with proximal humerus in claiming the last place in the sequence of epiphysial fusion.

For epiphysial chart, Group pattern of E.U.S. and a graph showing the sequences of fusion in the different families, please refer Figs. 31, 33 & 35.

THE STUDY OF EPIPHYSIS IN UNGULATA.

Ungulates are terrestrial animals with hoofs rather than claws or nails, and chiefly vegetarian in habit. The walk, although plantigrade in older types, becomes more and more digitigrade. There is a gradual perfection of the limbs as running and not climbing or grasping organs. Consequently, there is considerable modification of manus and pes. The interlocking of carpal and tarsal bones gives greater strength to the respective joints and makes the animal better fitted to run. In manus, the greatest number of complete digits is four, with occasionally a trace of the pollex; in the pes, four with never a trace of the hallux. The absence of digit No.1 is a characteristic of this group. With reduction of digits there is an elongation of metacarpals and metatarsals (metapodia). In the Ruminantia, the outer digits are very small and functionless (Cervidae) or entirely absent (Camelidae) and the metapodia of the persisting larger digits are united into a cannon bone. In Perissodactyla, digit No.4 is the largest and the gradual elongation of metapodia is manifest. The forms with broad tetradactyle feet are semiplantigrade and frequent places where the ground is soft. The majority, however, inhabit hard ground, are purely digitigrade, walk on the tips of their reduced toes encased in hoofs and are swift and active

TABLE NO.53
List of Artiodactyl skeletons.

Section Sub-Section Family Sub-Family.	Number of skeletons			Habits, special features etc.
	Total	Young	Adult	
Suidae	16	5+6(exp)	5	4 complete digits in manus & pes; digit 1 absent, 3 & 4 largest and reach ground; metapodia separate.
Hippopotamidae	2	1	1	Large heavy body; short tetradactyl limbs; all digits resting on ground. Amphibious.
<u>RUMINANTIA</u>	102	61	41	Metapodia 3&4 always united to a cannon; digits 2&5 always reduced and often absent.
Camelidae	10	3+1(Z)	6	Cannons cleft below; digitigrade ; has nails, not hoofs.
Tragulidae	4	2	2	4 complete toes, complete fibula.
<u>PECORA</u>	88	55	33	Horned; ulna & fibula reduced, metapodia 3&4 fused into a cannon.
Cervidae	25	11+1(Z)	13	
Giraffidae	4	3	1	Long limbs and necks.
Antilocapridae	1	-	1	
Bovidae	58	40	18	
Bubalinae	1	-	1	
Cephalophinae	4	2	2	
Antilopinae	3	1+2 (Z)	-	
Tragelophinae	3	2	1	Large bovine antelopes
Rupicaprinae	1	-	1	
Caprinae	38	18+12(exp)	7+1(exp)	
Bovinae	8	3	5	
Total	120	73	47	

<u>NOTE</u>:- (exp) denotes animals, the skeletons of which were obtained from experimental study. (Z) denotes young specimens obtained from Zoological Gardens, Edinburgh.

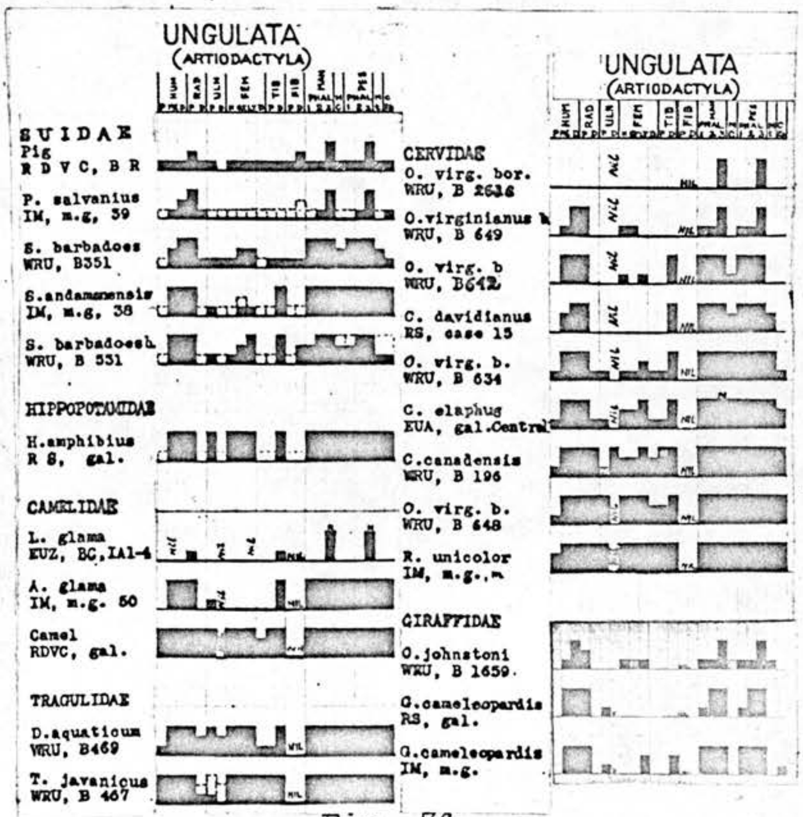


Fig. 36.

Epiphysial charts for the different Families of Artiodactyla, except Bovidae. Abbreviations as in other charts.

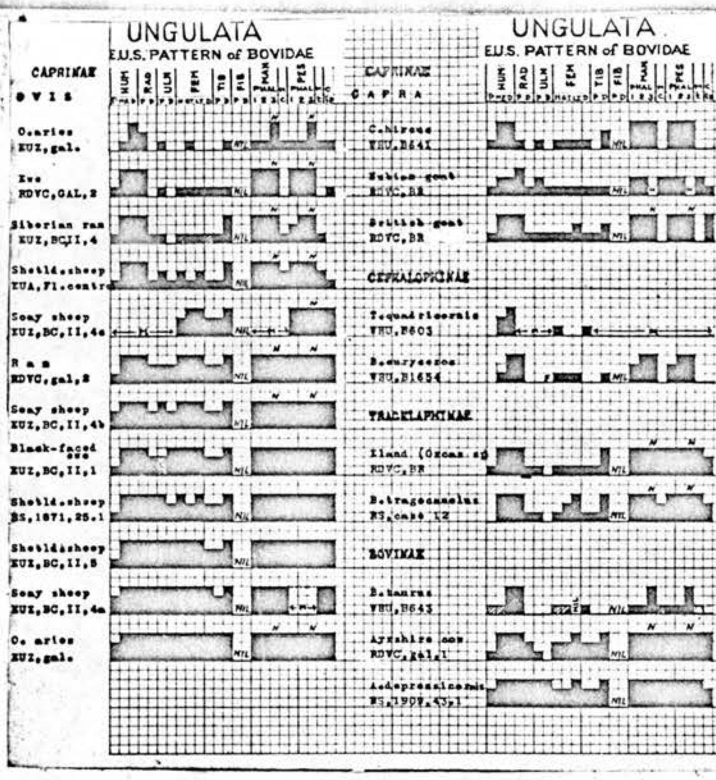


Fig. 37
Epiphysial charts showing the sequence of fusion of epiphyses in different sub-families of Bovidae. Abbreviations as before. 'N' stands for non-epiphysial ossification.

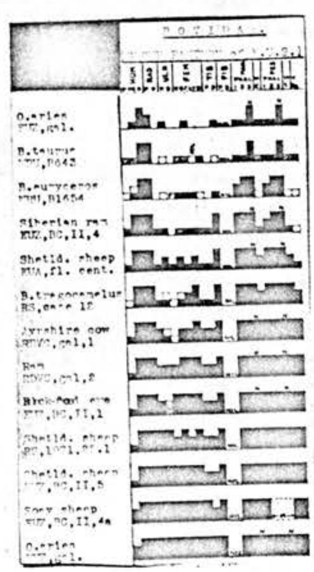


Fig. 38

Epiphysial chart showing the group-pattern of the Sequence of Epiphysial Fusion in Bovidae. Abbreviations as before.

runners. The ulna and fibula become rudimentary and fuse with the radius and tibia. The clavicle is always absent.

The existing Ungulates are divided into two Sub-Orders, the Artiodactyla and the Perissodactyla. Many authorities do not include Proboscidea and Hyracoidea in Ungulata, though in some features they agree.

A R T I O D A C T Y L A.

Digitigrade "even-toed" forms, with two prevailing digits symmetrical, namely, digits 3 & 4; axis of limbs passes between these (paraxonic); their metapodia are closely applied together or united into one cannon bone but having two medullary cavities. Digits tend to diminish in number. In higher forms only Nos. 3 & 4 persist. The pes is always ahead of manus in reduction and fusion of metapodia. Femur without a third trochanter. Fibula articulates with calcaneum and, like ulna, may be complete and distinct; but there is a tendency to reduction of both fibula and ulna, and fusion with tibia and radius. In Ruminantia, fibula is represented by lower end only (malleolar bone).

This Sub-Order consists of a number of families. Those available for the present study havebeen listed in Table No.53. (Epiphysial charts in Figs. 36,37,38).

Family SUIDAE.

Four completely developed digits in both limbs.

Pollex and hallux absent, digits 3 & 4 are larger than others and are symmetrical; digits 2 & 5 do not reach the ground in walking. Metatarsals and metacarpals are separate and are never completely fused together.

16 skeletons were studied. 5 of these have been listed in Table No.54. 6 were young specimens (Pigs Nos. 18,19,20,22,26 & 30) from Prof. Brash's experimental series of madderfed pigs (vide p. 27). Four of these were very young; their epiphyses were wide open. Nos. 18 & 19, however, showed the following epiphysial condition:-

	Pig No.18	Pig No.19
Non-union	Distal radius, ulna, femur; proximal femur, tibia and fibula.	Proximal tibia and fibula.
Beginning union	Proximal humerus and ulna; femoral trochanters; distal fibula and calcaneal epiphysis.	Proximal humerus and ulna; femoral trochanters; distal radius, ulna and femur.
Recent union	nil	Calcaneal epiphysis.
Complete union	Proximal and distal elements and epicondyles of humerus, distal epiphysis of humerus, proximal radius, distal tibia.	As in Pig No.18 plus proximal femur and distal fibula.

The remaining 5 were adult specimens consisting of a Sus scrofa (RS,C 15 & 16), 3 pigs (RDVC,gal,C 6) and a wart hog (RS, 1876, 55.1).

The incidence of fusion in the limb epiphyses of the younger skeletons was observed as follows:-

In skel.	RDVC, gal, 6	fusion of ep.	nil (term. phal. pes 'R')
" "	" BR, f further	" " "	5,17,32
" "	IM, m.g, 39, f "	" " "	9
" "	WRU, B351, m "	" " "	6,15,16,30,31
" "	EUA, pig No.18 "	" " "	3,7,8,24
" "	IM, m.g, 38 "	" " "	14,27,29
" "	EUA, pig No.19 "	" " "	18,26 (ep. 27 is 'R')

Hence the S.E.F. reads as follows:-

Terminal phalanges pes
Distal elements humerus, terminal phalanges manus
Proximal radius
Distal epiph. humerus, all prox. & middle phalanges
Prox. elements humerus, epicond. hum., dist. tibia
Metacarpals, metatarsals, calcaneal epiphysis
Head femur, distal fibula

Family HIPPOPOTAMIDAE.

Aquatic animals with amphibious habits; nostrils on surface of head; short limbs and tail, though the body is heavy and unwieldly. Tetradactyle, all digits reach ground and have nail-like hoofs. Ulna and fibula complete.

Only two specimens were available for study. One of these, H. amphibius (IM, m.g) was an adult and showed fusion of the whole ulna. The other (Table No.54) had the following epiphyses fused:-

3,5 to 9,14 to 18,24,26,27,29,32; & 11,19 & 20

The last three epiphyses were those that were found to have

Table No. 55

Order: UNGULATA Sub-order: Artiodactyla

Camelidae	Tragulidae		Cervidae					
Camelus	Hyomoschus or Dorcatherium	Tragulus	Cervulus	Cervus				
Camel	D.aquaticum	T.javanicus borneanus	C.roeveli	C.davidianus	C.elaphus	C.canadensis	Rusa Unicolor	molo alis
RCVC	W.R.U.	W. R. U.	R.S.	R.S.	E.U.A.	W.R.U.	I.M, m.g.	m.g.
Cal.	B469	B467	1877.10.1.	C15	floor	B193		
adult	Male Young adult	Male Young adult					Male Young adult	
x	x	x	x	x	x	x	x	
x	x	x	x	x	x	x	x	
+	+	+	+	+	+	+	+	
+	B	+	B	-	B	B	R	
+	+	+	+	+	+	+	+	
+	+	+	B	+	+	+	+	
+	+	+	R	nil ?	+	+	+	
+	+	+	R	R	+	+	+	
+	+	+	+	+	+	+	+	
+	R	B	B	-	B	+	+	
+	∓	B	B	-	B	- to B	+	
+	R	- (-)	-	-	-	+	+	
x	x	x	x	x	x	x	x	
+	+	+	B	R	+	+	+	
+	+	+	+	+	+	+	+	
+	+	+	+	+	+	+	+	
+	+	+	+	+	+ or nil	+	+	
+	+	+	B	-	R	R	+	
+	+	+	L	-	R	R	+	
+	+	+	D	-	+	+	+	
R	B or - (Todd)	+	-	-	B	R	+	
+	B or - (Todd)	+	-	-	B	R to +	+	
+	B	+	-	-	B	B	+	
+	+	+	B	+	+	+	+	
+	x	x	x	x	x	x	x	
x	x	x	x	x	x	x	x	
+	+	+	R	-	R	+	+	
x	x	x	x	x	x	x	x	
+	+	+	D	R	+	+	+	
+	+	+	+	+	+	+	+	
+	+	+	+	+	+	+	+	
+	+	+	+	+	+	+	+	
c. skel.		V.great leapers. Hind limbs v.long comp. to fore esp. tibia & hind cannon.				Zoo sp.	Artic. skel. not dis-articulable.	
.3.3 / 3 3 worn		0.1.3.3 / 3 1 3 3 much worn			0.1.3.3 / 3 1 3 3	0.1.3.3 / 3 1 3 3 slight wear	0.0.33 / 3 0 3 3 much worn	M

Femur (proximal)

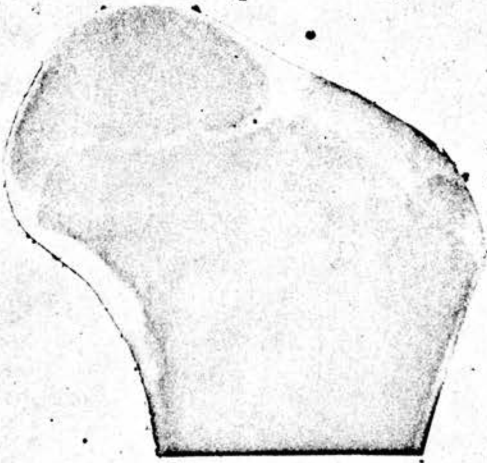
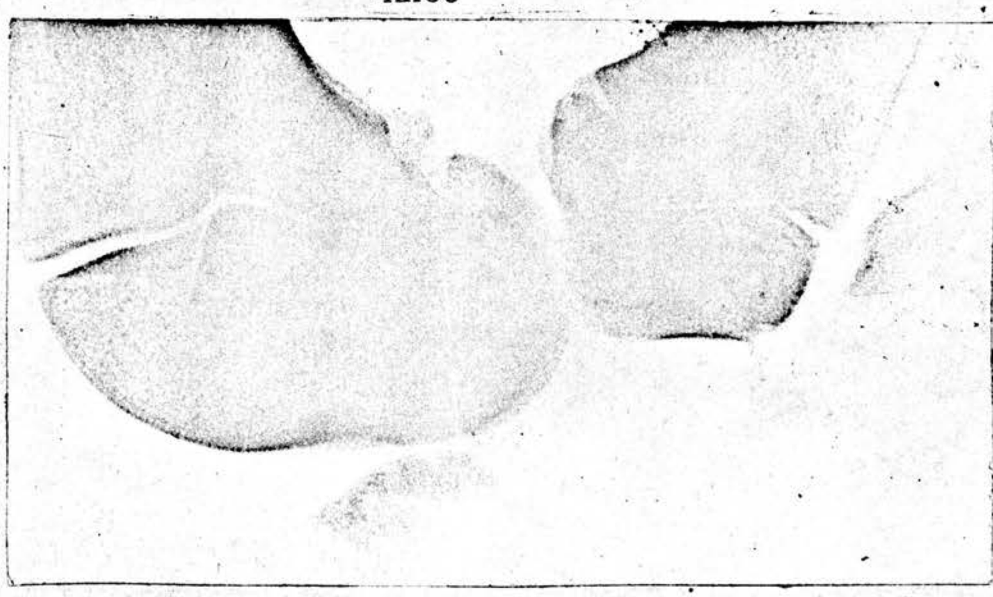


Fig. 39.
(contd.)

Knee



Ankle

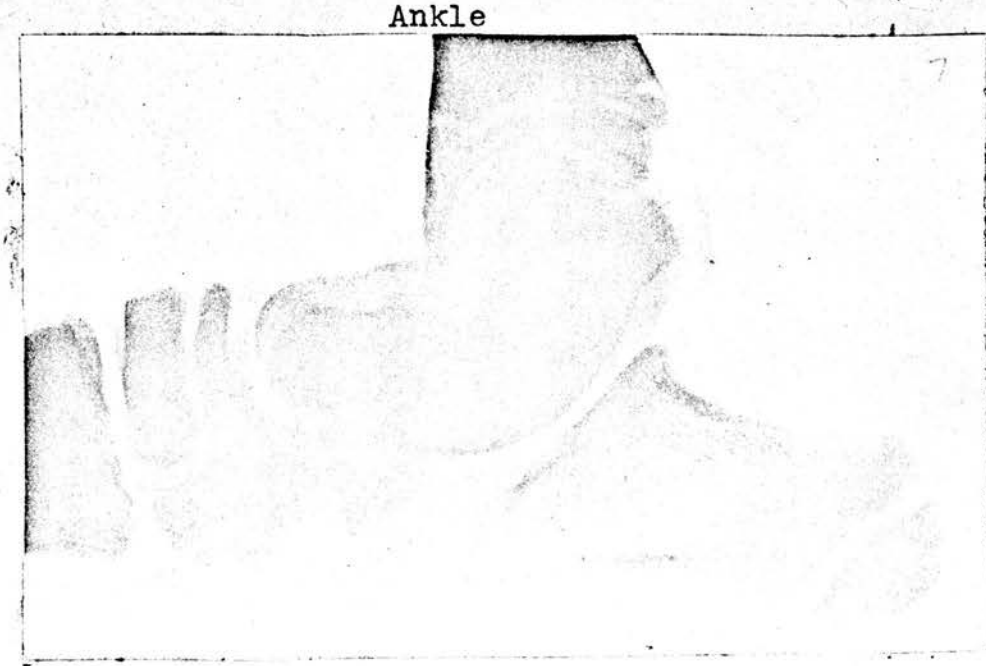
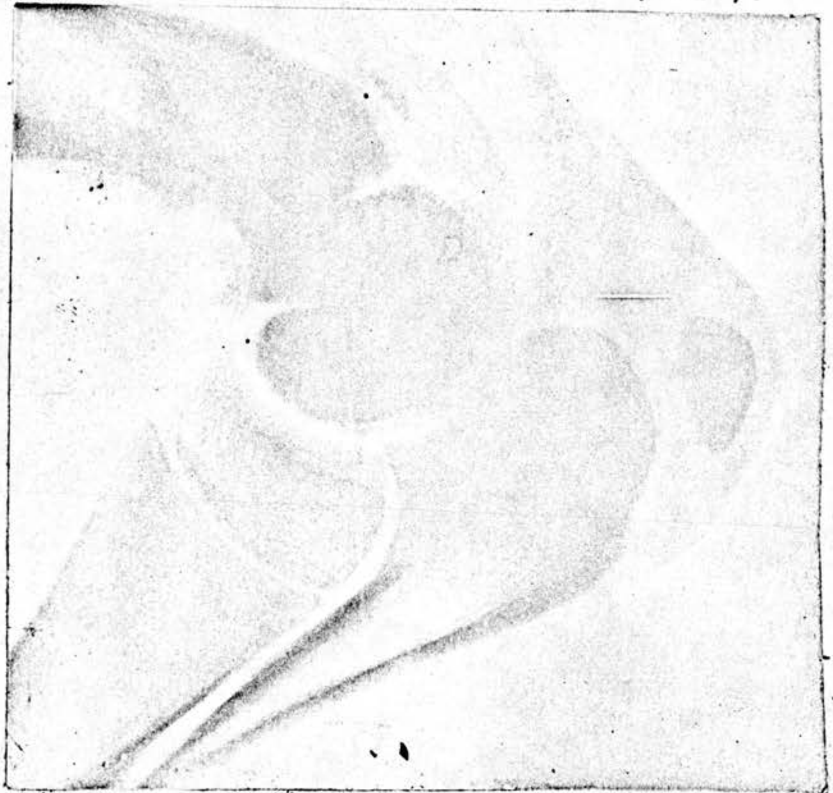
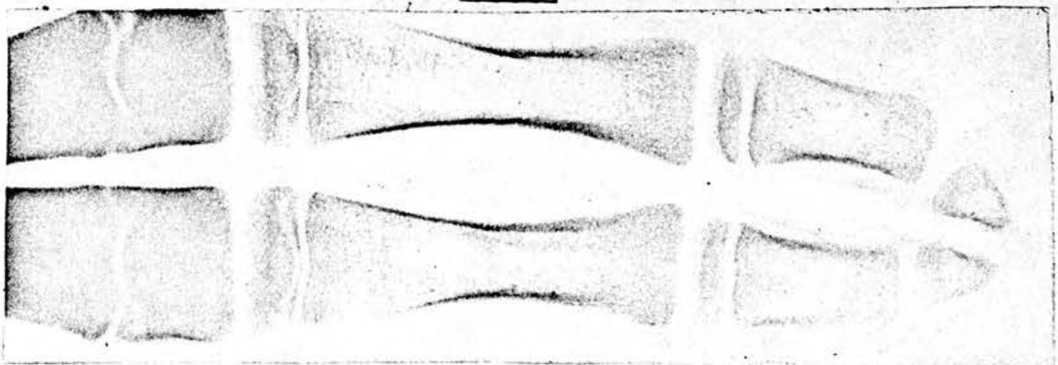


Fig. 39.

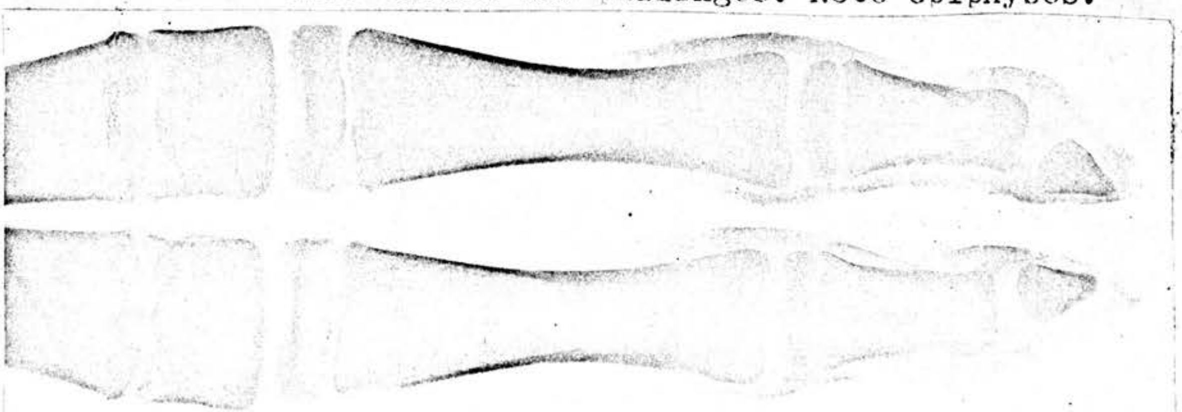
Radiographs of a new born camel (male).



Elbow



Fore cannon and phalanges. Note epiphyses.



Hind cannon and phalanges. Note epiphyses.

fused in addition to the ones noted in Suidae. Fusion of proximal ulna and femoral trochanters may, therefore, be considered to form the next step in the scale of fusion.

Section RUMINANTIA.

It represents ruminating Artiodactyls; metapodia 3 & 4 united to a cannon bone, digits 2 & 5 reduced or absent. The group comprises Camelidae, Tragulidae and Pecora.

Family CAMELIDAE.

Ulna reduced or ankylosed to radius; fibula reduced and represented by malleolar bone only; digitigrade on cushion-like pads; didactyle, cannon cleft below; digits with nails, not hoofs.

4 young skeletons were studied. 3 of these have been listed in Tables Nos. 54 & 55. The 4th was supplied by the carcass of a newly born camel from the Costorphine Zoo, Edinburgh (vide p.27). Flesh was removed from this body and the bones studied macroscopically and with X-rays for evidence of epiphysial centres (see Fig. 7, facing p. 39 and Fig. 39). All the epiphyses were wide open. The terminal phalanges had no epiphyses.

Besides, 6 adult skeletons had completed fusion of all limb epiphyses, viz:

2 lamas (EUZ, MM 23 & MM 24 and EUZ,BC,V,1),
1 vicuna (EUZ,BC,V,1), 1 alpaca (EUA,44V)* and
2 bactrian camels (IM,m.g,1; RS, floor,1).

The following fusion was observed:-

In skel. EUZ,BC,1,A1-A4		fusion of ep.	5,17?,32?
" " IM,m.g,50	further	" " "	3,6 to 9,14 to 17,24, 29 to 32
" " RDVC,gal	"	" " "	11,18,19,20,27 & 4,10,12,22,23
Presumably the last to fuse would be		"	21

From the above it is seen that the S.E.F. of camels shows no difference from Suidae and Hippopotamidae up to the stage studied in the latter. A further stage of fusion is, however, seen in the camel, viz:

Distal radius and ulna, proximal tibia and humerus, and the only member remaining to fuse is the

Distal femur.

Family TRAGULIDAE.

Very small animals; 4 complete toes, metapodia 3 & 4 uniting late; complete fibula ankylosed at distal end with tibia.

4 skeletons were studied, 2 of which were adults, viz: Tragulus kanchil (IM,m.g,39) and Hyomoschus aquaticus (RS, C 16).

The following fusion was observed:-

In skel. D. aquaticus, m (WRU,B469)		fusion of ep.	3, 5 to 9, 11, 14 to20 24,27,29 to 32
" " T. javanicus borneanus, m (WRU,B647)	further	" " "	4,21,22,23 (but ep.10 & 11 are 'B'; ep.12 is '-')

Presumably the last to fuse would be ep. 10 or 12, probably ep. 12.

Todd & Todd[81] had studied the same two animals (WRU, B469 & B467) for their article, "The Epiphysial Union Pattern of the Ungulates with a note on Sirenia". Chart I on p. 26 of the article shows that in skeleton, WRU, B647, the radius and ulna are "missing". The present worker, however, when studying the same material at WRU, found 2 radii and 2 ulnae along with skeleton B647, all of them being marked as in the rest of the skeleton with the distinctive number 'B647'. It is hard to believe that the late Prof. T. W. Todd, who was exceptionally careful about his osteological collections would have allowed wrong labelling. It is however apparent that the sequence that these writers sought to draw in their chart and the analysis they gave in their text would have suffered by inclusion of the condition of fusion as observed by the present worker in the radius and ulna of this skeleton.

Hence, the last step in the fusion in Tragulus includes ep. 12 or 10 and excludes ep. 21.

Sub-Section PECORA.

Ulna reduced and fixed behind radius. Fibula reduced to malleolar bone. Metapodia 3 & 4 fused to form a cannon. Digits 2 and 5 often absent.

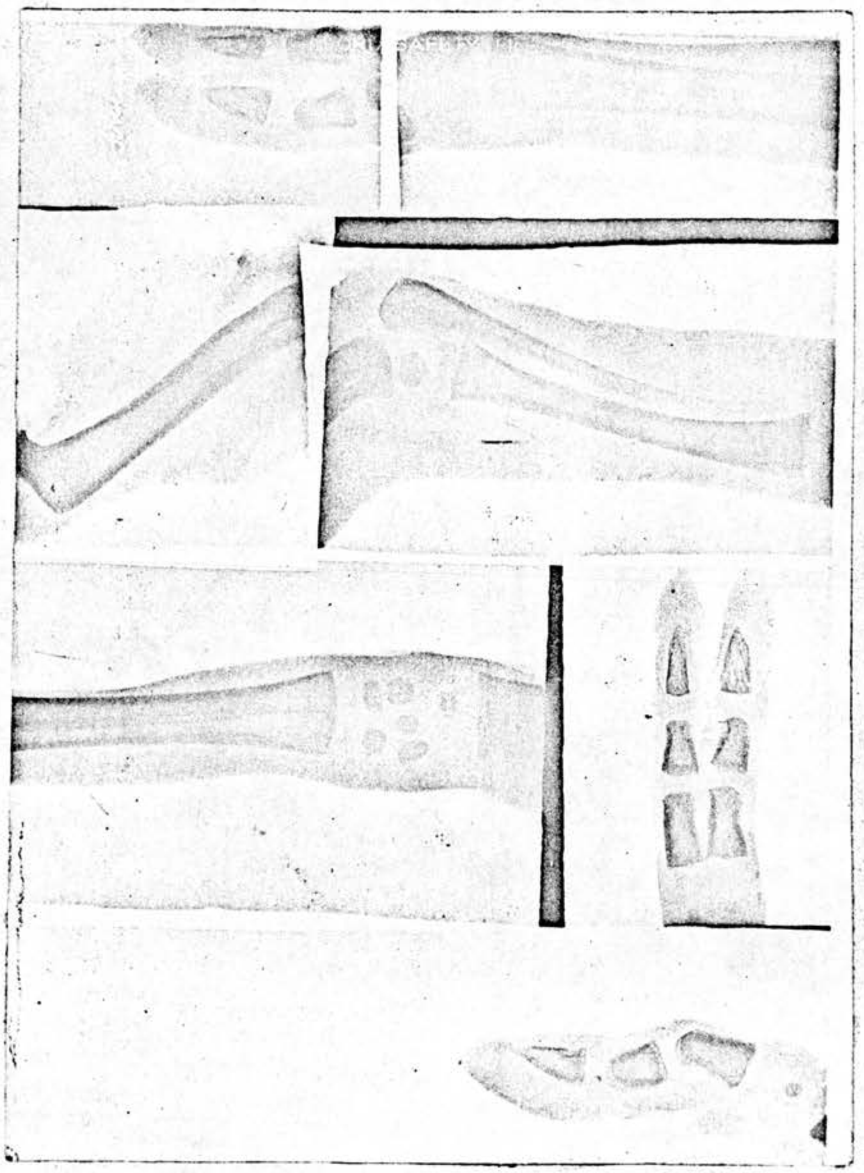


Fig. 40.

Radiographs of the left fore-limb of a still-born deer showing the epiphyses present at birth.

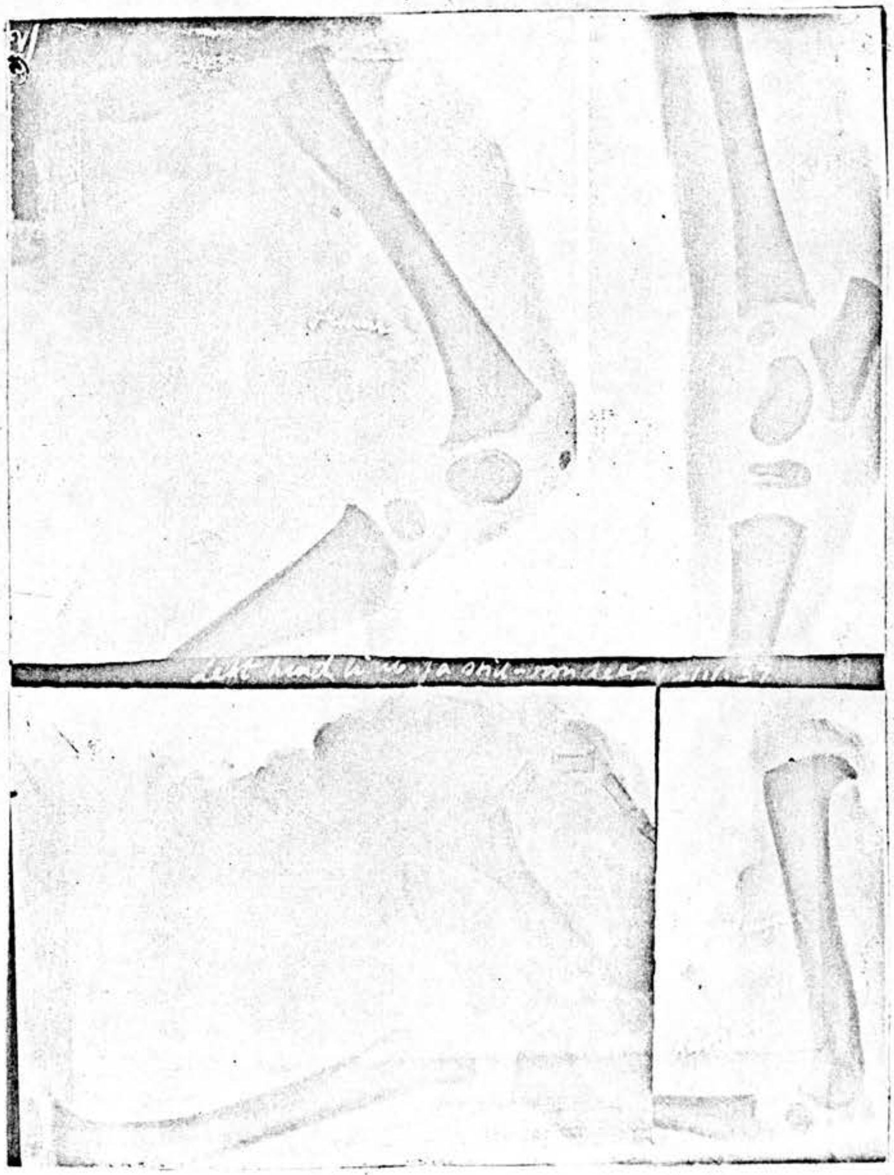


Fig. 40 (contd.).
Radiographs of the left hind limb of a still-born deer showing the epiphyses present at birth.

It comprises 4 families; Cervidae (deer), Giraffidae, Antilocapridae and Bovidae (sheep, goats, oxen etc.)

Family CERVIDAE:

Outer digits usually present, though small, their metapodia reduced and often fused with the cannon bone.

25 skeletons were studied. 10 of these have been listed in Tables Nos.55 & 56. Details of specimen, WRU, B2616 have been copied from Todd & Todd[81]. One was a still-born deer from the Costorphine Zoo (see p. 27). Its epiphyses were studied macroscopically and under X-rays (Fig. 40). The rest were adult skeletons as follows:-

In WRU, Odocoileus virginianus; B633,f & B78,f. Cervus B 195. Hydropotis inermis, m; B606. Muntiacus muntiac vaginalis,m; B607.

In EUA, Roe deer; 44, VI & 44,VII. Japanese deer; 44, VIII. Fallow deer; 44,XXXIV.

In IM, Barking deer; m.g,50. Rusa unicolor; m.g,55.

In RS, Moschus moschiferus; Case 16.

In EUZ, Alces machilis; MM 35 & MM 36.

The incidence of epiphysial fusion in the 11 young animals (Tables Nos.55 and 56) and in the new-born deer may be seen in the following:-

Table No. 56

Order: UNGULATA . Sub-order: Artiodactyla Div: Pecora

Cervidae						Giraffidae		
Odocoilus or Cariacus						Okapia	Giraffa	
O. virginianus	O. virg.	O. virg.	O. virg.	O. virg.	O. virg.	O. johnstoni	G. camelopardalis	G. camelopardalis
W.R.U.	W.R.U.	W.R.U.	W.R.U.	W.R.U.	W.R.U.	W.R.U.	R.S., gal,	I.M., m.g.
B2616	B639	B649	B642	B634	B648	B1659	floor	
Male v. young	Male young	Male young	Male young	Fem. 6 yrs.	Fem. above 2 yrs.	Fem. young		Male young
x	x	x	x	x	x	x	x	x
x	x	x	x	x	x	x	x	x
-	-	-	B	B	+	B	+	+
-	-	-	-	B	B	-	-	-
-	+	+	+	+	+	+	+	+
-	+	+	+	+	+	+	+	+
-	B	B	+	+	+	B	+	+
-	B	B	+	+	+	B	+	+
-	+	+	+	+	+	R	+	+
-	-	-	-	B	+	-	-	-
-	-	-	-	B	+	-	B	B
-	-	-	-	-	-	-	-	F
x	x	x	x	x	x	x	x	x
-	M	-	- to B	+	+	- to B	-	-
-	M	- to B	+	+	+	B	B	+
-	M	B	+	+	+	B	+	+
+	M	+	+	+	+	+	+	+
-	-	B	B	B	+	B	-	-
-	-	B	-	B	+	B to -	-	-?
-	-	-	B	R	+	B	-	R
-	-	-	-	B	R	-	-	-
-	-	-	-	B	R	-	-	B
-	-	-	-	B	L.U.	-	-	-
-	-	-	+	+	+	-	-	R
	complete absence.							
-	M	-	-	- to B	+	-	-	B
x	M	x	x	x	x	x	x	x
-	M	-	-	+	+	- to B	-	-
-	M	- to B	+	+	+	B	B	+
-	M	B	+	+	+	B	+	+
+	M	+	+	+	+	+	+	+
		Middle of 2nd period of life	2nd period of life		extreme end of 2nd period of life			Articulated skeleton
From Todd & Todd, Am.J.Anat. 1938, V.63, pp 27	zoo spec. upper teeth and jaw badly diseased	zoo sp.	zoo sp.		zoo sp.			
		0.0.3.3 / 3 1 3 3 M_3's in crypt	0.0.3.3 / 3 1 3 3 M_3's in	0.0.3.3 / 3 1 3 3 M_3 in	no skull	M_2 eruption, dm's in place	0.0.3.3 / 3 1 3 3 lower dm 1 & 2 still in, M_3's in crypt	

(a) In the old-world deer

In new-born deer, EUA		fusion of ep. nil
In skel. RS, 1877, 10.1		" " " 3,5,9,15,16, 17,30,31,32
" " C. davidianus; RS,C15	further	" " " 6,24
" " C. elaphus; EUA,floor	"	" " " 7,8,14,20,29
" " WRU, B195	"	" " " 10,12,27(18, 19,21 are 'R')
" " Rusa unicolor, m;IM,m.g,	"	" " " 11,18,19,21, 22,23
Presumptively,last to fuse would be		" 4

(b) In the new-world deer, Odocoileus virginianus borealis, of which there was a graded collection in the WRU:-

In skel. WRU,B2616,m		fusion of ep. 17, 32
" " " B639,m & B469,m	further	" " " 5,6,9
" " " B642,m	"	" " " 7,8,15,16,24, 30,31
" " " B634,f	"	" " " 14, 29
" " " B648,f	"	" " " 3,10,11,18,19, 20,27
Presumably the last to fuse would be		" 4,12,21,22,23

Grafting the sequences as found in the above two species, the following sequence may be arrived at:-

Ep. 17,32	i.e.	terminal phalanges, all
" 5,9	"	ele.dist. ep. hum.,prox. radius
" 6 (new-world forms)	"	dist. ep. and shaft humerus
" 15,16,30,31	"	middle & proximal phalanges, all
" 3 (old-world forms)	"	elements proximal ep. humerus
" 24,6(old-world forms)	"	dist. tibia; ele. dist. hum.
" 7,8	"	lat. & med. epicond. humerus
" 14,29	"	metacarpals, metatarsals
" 20,3 (new-world forms)	"	lesser troch. fem;prox.ele.hum.
" 27,10,12(old-world ") " 11,18,19	"	calc. ep.,dist. rad.,dist. ulna, prox.ulna,prox.fem.,gr. troch.
" 21,22,23,12(n.w.forms)	"	dist.fem.,prox. tib.,dist. ulna
" 4	"	prox. humerus

M_2 & M_3 erupting 3 1 3 3 3 1 3 3 3 0 3 3 3 1 3 3

In the above, ep. 11,18 and 19 have been put together with ep. 27, 10 and 13 since the former were in 'R' stage and almost indistinguishable from '+'

Family GIRAFFIDAE:

Long limbs, long necks, digits 2 & 5 entirely absent.

4 skeletons were studied, of which one was an adult (Okapia johnstoni, m; WRU, B894). The rest (Table No.56) showed the following incidence of epiphysial fusion:

In skel.	WRU, B1659	fusion of ep.	5,6,17,32
" "	G. cameleopardis (RS,gal) further	" " "	3,7,8,9,16,31
" "	" , m(IM,m,g) "	" " "	15, 30

Family ANTILOCAPRIDAE: Only 1 adult skeleton was available (Antilocapra americana; WRU, B1527) in which all limb epiphyses were fused.

Family BOVIDAE:

Lateral digits usually present. There are many sub-families.

Sub-Family Bubalinae: Large African antelopes. Only 1 adult skeleton studied (Gorgon taurinus, m; IM, m.g,50).

Sub-Family Cephalophinae: Small or medium antelopes.

4 skeletons studied, 2 being adult (Cephalophus leucogaster; RS, 1935, 22.18 and Tetraceros quadricornis, m; WRU, B 1326).

skull M_1 stage M_2 & M_3 erupting No skull 3 1 3 3 3 1 3 3 3 0 3 3 No skull 3 1 3 3

Table No. 57

Order: **UNGULATA** Sub-order: **Artiodactyla** Div: **Pecora**

Family	Bovidae								
S.Fam.	Caprinae								
Genus	Ovis								
Name	Lamb	O.aries	Ewe	Fat-tailed sheep	Siberian ram	Shetland sheep	Ram	Spay Sheep	Black-faced ewe
Museum	W.R.U	E.U.Z	RDVC	E.U.Z	E.U.Z	E.U.A	RDVC	E.U.Z	E.U.Z
Number	B330	gal.	gal,2	BC,I14	BC,I14	floor	gal,2	BC,II,4C	BC,II,1
Sex			Fem.		Male		Male	Male	Fem.
Age	juvenile (5 weeks)	young	young						
EPIPHYSES									
Clav, St....	Never present								
Ac....									
Hum, Pr.El.	-	B	B	+	+	R	+		+
" & Sh.	-	-	B	B	B	B	B		B
Di.El.	-	+	+	+	+	+	+		+
" & Sh.	-	B	+	+	+	+	+		+
Lat.Ep.	-	B	+	+	+	+	+		+
Med.Ep.	-	B	+	+	+	+	+		+
Rad, Prox..	-	R	+	+	+	+	+		+
Dist..	-	-	-	-	B	B	R		R
Ulna, Prox..	-	B	B	B	B	R	R		R
Dist..	-	-	-	-	-	B	R		+
Mc, First.	absent								
Rest..	-	B	-	B	B	R	+		+
Ph(M), Prox..	-	B	+	+	+	+	+		+
Mid...	-	B	+	+	+	+	+		+
Term..	B	+ or nil	+ or nil	+ or nil	+ or nil	+ or nil	+ or nil		+
Fem, Head..	-	-	B	B	- to B	R	+	R	+
Gr.Tr.	-	B	B	B	B	B	+	+	+
Ls.Tr.	-	-	B	B	B	R	+	+	+
Dist..	-	-	B	B	- to B	B	R	R	R
Tib, Con...	-	-	B	B	B	B	R	R	R
Tb....	-	-	-	B	-	B	B	R	R
Dist...	-	B	B	R	+	+	+	+	+
Fib, Prox..	absent								
Dist..									
Calc. Epip..	-	B	B	B	-	B	+	+	+
Mt, First.	absent								
Rest..	-	B	-	B	B	R	+	+	+
Ph(P), Prox..	-	B	+	+	R	+	+	+	+
Mid...	-	B	+	+	+	+	+	+	+
Term..	B	+ or nil	+ or nil	+ or nil	+ or nil	+ or nil	+ or nil	+ or nil	+
Ext.Centres..									
SPL.FEATURE.									
HABITS ETC..									
REMARKS.....		sp. ligamentous						lower limb only	
DENTITION...	No skull	M_1 stage M_2 & M_3 erupting		No skull	0.0.3.3 / 3 1 3 3	0.0.3.3 / 3 1 3 3	0.0.3.3 / 3 0 3 3	No skull	0.0.3.3 / 3 1 3 3

The others (Table No.57) showed:-

In skel. WRU, B1654,m fusion of ep. 5,6,9,16,17,31,32

" " " B603,m further " " " 7

Sub-Family Antilopinae: 3 specimens studied. 2 consisted of a 2-day old and a 16-day old antelope sent from the Costorphine Zoo (vide Fig. 4 & p. 27); their epiphyses were studied under X-rays. The other (Table No.57; EUZ, BC, 1, B1-B4) was too young to have any epiphysis closed. There was no epiphysis in the terminal phalanges of its fore-limbs; those of the hind limb being covered by hoof could not be examined properly.

Sub-Family Tragelaphinae: Large bovine antelopes.

3 specimens studied, 1 of which (Boselaphus tragocamelus; IM, m.g) was an adult. The rest (Table No.57) showed the following:-

In skel. B. tragocamelus (RS, C12) fusion of ep. 3,5 to 9,15,16,17,20,24,29,30,31,32

" " Eland (RDVC, BR) further fusion of ep. 14

NOTE: Existence of ep. at terminal phalanges was doubtful.

Sub-Family Rupicaprinae: Intermediate between antelopes and goats. Only 1 adult skeleton was available (Budorcas taxicolor; IM, m.g).

Sub-Family Caprinae: Sheep and goats; essentially mountain animals. The study consisted of 30 young animals (including

Table No. 58

UNGULATA — Artiodactyla — Div: Pecora

Bovidae Cephalophinae		Antelopinae	Tragelaphinae			Caprinae	
Boo-ceros	Tetra-ceros		Bose-laphus	Orcas		Capra	
B.eury-ceros	T.quadri-cornis	Antelope	B.trago-camelus	Eland	Nubian goat	C.hircus	British goat
W.R.U.	W.R.U.	E.U.Z.	R.S.	RDVC	R.D.V.C	W.R.C.	R.D.V.C.
B1654	B603	BC,18_{1-4}	C.12	B.R.	B.R.	B641	B.R.
Male	Male					Fem.	Male
young	young					adoles-cent	1 yr.9 months
N e v e r p r e s e n t							
-	B	-	R	+	B	+	+
-	-	-	-	B_	B	B	B
+	+	+	+	+	+	+	+
+	+	-	+	+	R	+	+
B	+	-	+	+	R	+	+
B	R	-	+	+	R	+	+
+	M	-	+	+	+	B	+
-	M	-	B	B	B	-	B
-	M	-	B	B	R	B	B
-	M	nil	-	-	B	-	B
		a b s e n t					
-	M	-	R	+	R	-	-
R	M	-	+	+	R	+	+
+	M	-	+	+	R	+	+
+	M	?	+	+ or nil	M	+	+ or nil
B	B	-	-	B	B	B	B
B	-	ot.	R	B	B	B	B
B	-	-	+	B	B	B	R
-	B	?	B	B	R	B	B
-	M	-	B	B	B	-	B
-	M	-	R	B	B	-	B
-	M	B	+	+	B	R	R
		a b s e n t					
-	M	-	R	R	B	-	+
		a b s e n t					
-	M	-	+	+	R	-	-
R	M	-	+	+	R	+	+
+	M	-	+	+	R	+	+
+	M	B covd. by hoof	+	+ or nil	M	+	+ or nil
sp. ligamentous		limbs only examined					
Stage of union of elbow ep.						bad nutrition	
			0.0.3.3 / 3 1 3 3	Skull M 3,1,3,2 M_3 not in	0.0.3.2 / 3 1 3 2 M_3 not in	0.0.3.2 / 3 1 3 3 M_3 in slight wear	Skull & Jaw M

Table No. 59

Order: UNGULATA Sub-order: Artiodactyla Div: Pecora

Bovidae Caprinae Ovis						Bovinae Anoa	Bos	
Shetland sheep	Shetland sheep	Spay sheep	Spay sheep	Spay sheep	O.aries	A.depressicornis	B.taurus	Ayrshire cow
R.S. 1871,25.1	E.U.Z. BC,II,5	E.U.Z BC,II,4 B	E.U.Z BC,II,4 Fem.	E.U.Z BC,II,4A	E.U.Z gal. Male	R.S. 1909,43.1	W.R.U. B643 Male 2 yrs.	R.D.V.C gal,1 Female young
Never present								
+	+	+	+	+	+	+	L.U.	+
B	B	R	R	R	R	R	- to B	B
+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	B	+
+	+	+	+	+	+	+	- to B	+
+	+	+	+	+	+	+	+	+
+	+	R	+	+	+	+	-	R
+	+	+	+	+	+	+	-	B
R	+	R	+	+	+	+	-	-
absent								
+	+	+	+	+	+	+	- to B	+
+	+	+	+	x	+	+	B	+
+	+	+	+	x	+	+	B	+
+	+	+ or nil	x	+ or nil	+	+	+	+ or nil
+	+	+	+	+	+	R	- to B	R
R	+	+	+	+	+	R	- to B	R
+	+	+	+	+	+	+	ct.	+
R	R	R	+	+	+	R	B	R
R	R	R	+	+	+	R	B	R
B	B	R	R	+	+	R	-	R
+	+	+	+	+	+	+	-	+
absent								
+	+	+	+	+	+	R		+
absent								
+	+	+	+	+	+	+	- to B	+
+	+	+	+	M	+	+	B	+
+	+	+	+	M	+	+	B	+
+	+	+ or nil	+ or nil	M	+	+	+	+ or nil
							case of lapsed growth.	
Standard	Stand.	no skull	$\frac{0.0.2.3}{3\ 1\ 2\ 3}$	M	Stand.	$\frac{0.0.2.3}{3\ 1\ 3\ 2}$	M_2 cut M_3 in crypt	$\frac{0.0.3.3}{3\ 0\ 3\ 3}$

12 animals from the study of abnormal and experimental series of Todd, Simpson and Liddell, (vide Tables Nos. 60 and 61) and 8 adults including 1 control animal (WRU B1058,f Table No.61). The other 7 adults were, 2 Capra hircus (WRU, B640,m and B 840,f); Soay sheep (RS, 1932,87); St. Kilda sheep,f (EUZ, BC, II,1); Ovis vignei, m (IM, m.g, 50); Ovis ammon (IM, mg); O. aries (WRU, B833).

The incidence of epiphysial fusion in the 18 normal animals (Tables Nos. 57,58 & 59) was:-

Goats

In skel.	Nubian goat (RDVC,BR)		fusion of ep. 5,9,(term. phals. missing)
" "	WRU, B641,f	further	" of ep. 3,6,7,8, 15,16,(17) 30,31, (32);(9 is 'B')
" "	British goat(RDVC,BR)	"	" of ep. 27 (existence of ep. term. phal. doubtful)

Sheep

In skel.	WRU, B330		" of ep. nil
" "	O. aries(EUZ,gal)	"	" " " 5,17 ?, 32? (existence of ep. 17 & 32 doubtful).
" "	Ewe (RDVC, gal,2)	"	" of ep. 6 to 9,15, 16,30,31
" "	Fat-tailed sheep (EUZ, BC,II,4)	"	" " " 3
" "	Siberian ram (EUZ,BC,II,4) & Shetland Sheep(EUA, floor)	"	" " " 24

In skel.	Ram (RDVC,gal,2) & Soay sheep, lower limbs only (EUZ, BC, II, 4C)	further fusion of ep. 14,18,19, 20,27,29
" "	Soay sheep (EUZ, BC,II,4B)	" " " " 11
" "	Black-faced ewe (EUZ,BC,II,1)	" " " " 12
" "	Shetland sheep (RS,1871,28.1) & (EUZ,BC,II,5)	" " " " 10(ep.12 & 19 are 'R' in sk. RS, 1871, 28.1)
" "	Soay sheep, f (EUZ,BC,II,4)	" " " " 21, 22
" "	Soap sheep (EUZ,BC,II,4A) & O.aries,m (EUZ,gal)	" " " " 23

Presumably the last ep. to fuse would be ep. 4.

Comparing the S.E.F. for goats and sheep, that for Caprinae as a whole may be presumed to be:-

5,17,32	i.e.	dist. el. hum. & term. phal.
9	"	prox. radius
6,7,8,15,16,30,31	"	epicond. & dist. ep. hum., prox. & middle phalanges
3	"	prox. elements humerus
24	"	distal tibia
27	"	calc. ep.(in goats)
14,18,19,20 & 29	"	metacarps., metatars., prox. femur & trochanters
11	"	prox. ulna
12	"	dist. ulna
10	"	dist. radius
21,22,23	"	dist. femur & prox. tibia
4 (presumably)	"	prox. humerus

<u>Sub-Family Bovinae:</u> Of 8 skeletons studied, 5 were of adult animals, viz: Bos gaurus (IM, m.g, 495 G; and IM, m.g, 495 I), Bos frontalis (IM, m.g), American bison (EUA, floor, 7; and RS, floor). The remaining three (Table No.59) showed:-

In skel.	WRU, B643,m	fusion of ep.	3,5,6,9,17?,32?
" "	Ayrshire Cow (RDVC,gal,1)	further " " "	7,8,14,15,16,20, 24,27,29,30,31
" "	RS, 1909, 43.1	" " " "	10,11,12 (27 is 'R')

Hence, the ep. awaiting fusion are 18 & 19; 21 & 22, (23);&4

Koch[83], from an exhaustive study of 53 European bisons (Bos bonasus L. of Lithuanian breed), gives the following sequence:-

Distal humerus & epicondyles humerus	i.e. ep. 6,7,8
Distal tibia	" " 24
Head radius, calc. ep., metacarpal) & metatarsal epiphyses)	" " 9,27,14,29
Olecranon	" " 11
Head & greater trochanter femur	" " 18,19
Proximal tibia & distal femur	" " 22, 21
Distal radius & ulna	" " 10, 12
Head humerus	" " 4

<u>DISCUSSION</u>:

The sequence of epiphysial fusion in the different sub-families of Bovidae may be represented side by side and a tentative pattern may be chalked out which would perhaps, with very minor modification, give an average picture of the sequence in the whole family. Terminal phalangeal epiphyses where not traceable are taken as fused.

Cephalophinae	Caprinae	Bovinae: Bison (Koch)	Bovinae: All (Basu)	BOVIDAE (Average)
5,6,9,16,17, 31,32	5,17,32	6,7,8	3,5,6 9,17,32	5,17,32
	9			9
		24		
	6,7,8,15, 16,30,31	9,14,29	7,8,14, 15,16, 20,24, 27,29, 30,31	6,(3 in Bovinae)
	3	11		
				16,31
Tragelaphinae	24	18,19		
			10;11,12	7
	27	22,21		
				8,15,30
3,5 to 9, 15,16,17, 20,24,30, 31,32 & 29	14,18,19, 20 & 29	10,12	18?, 19? & 21,22,23, & 4 (Hypothetical)	
				3
	11	4		
				24 (27 in goats)
14	12			
	10			29,20
	21,22,23			14
	4			27,18,19
				11
				12
				10
				(18?,19? in Bovinae)
				21,22,23
				4

In the above, it is seen that there is a slight acceleration in the fusion of proximal elements of humerus in Bovinae, which is not much significant. In Koch's series there is considerable retardation of proximal radius. It may be, according to Todd and Todd[81], an indifferent appraisement. But the acceleration of distal tibia over proximal radius and proximal femur, metacarpals and metatarsals is significant, since it is seenin Tragelaphinae, Caprinae and Bovinae. A similar condition was met with in Mus decumanus (vide p.114) and Myomorpha (vide p.116), both by Todd and the present writer. The retardation in fusion of head and greater trochanter of femur in Bovinae to a stage later than the fusion of distal radius and distal ulna is not unusual, as it is also met with in Cervidae (vide infra). The retardation, noted in this work, is based on observation on three skeletons only, whereas Koch's figures based on fiftythree do not show the same. Two of the three specimens showed 'R' stage of union for the femoral head. It may be considered as practically fused, since it is known that epiphyses remain in 'R' stage for a long time before the delicate line at diaphyso-epiphysial separation is finally wiped off and that no addition to the length of the bone takes place in the meantime. On this basis, the findings of the writer of the later stages of epiphysial fusion in Bovinae would be more in line with those of Koch, proximal femur preceding distal radius and proximal and distal ulna.

The acceleration of Calcaneal epiphysis in goats is not much significant except that its early fusion is a reminder of the mountaineering habits of the animal.

Comparison may now be taken up with the other families of Pecora, Ruminantia and Artiodactyla.

The S.E.F. in Pecora represented by symbols is as follows:-

Cervidae. (average)	Giraffidae.	Antilo-capridae.	Bovidae. (average)
17,32	5,6,17,32	no observation.	5,17,32
5,9	3,7,8,9,16,31		9
6	15,30		6(3 in Bovinae)
15,16,30,31			16,31
3			7
24,(6 in o.w.)			8,15,30
7,8			3
14,29			24(27 in goats)
20 (3 in n.w.)			29,20
27,10,(12 in o.w)			14
11,18,19			27,18,19
12,21,22,23			12
4			10
			(18?,19? in Bovinae)
			21,22,23
			4

NOTE: "o.w." & "n.w." indicate old-world and new-world forms.

The incidence of fusion in Giraffidae is incomplete for want of materials. Fusion of humeral epicondyles (ep.7 and 8) is distinctly retarded in Cervidae. The S.E.F. in Cervidae and Bovidae, however, is very nearly similar except that,in the very fleet-footed deer,distal radius (ep. 10) fuses earlier and even before proximal femur, making their wrists stronger and more capable of bearing strain at an earlier period of their life.

In the light of the above, the S.E.F. in Camelidae (vide p.146) and the superimposed S.E.F. of Suidae and Hippopotamidae (vide p.144) may be shown as follows:-

<u>Camelidae</u>

5; 17,32
3,6,7,8; 9;
15,16,30,31;
24; & 14,29
11; 18,19,20;
10,12; 22,23;
4
21

<u>Suidae</u>

32
5,17
9
6,15,16,30,31
3,7,8; 24
14,29; 27
26; 18

<u>Hippopotamidae</u>

19,20; 11

An average S.E.F. in Artiodactyla minus Tragulidae is now arrived at, and is as follows:-

32
17
5
9
6
16,31
(7)
15,30
7,8
3
24
29
14,20
27,(10,12)
26; 18
19
11
10,12
22,23;
21
4 (21)

Tragulidae is zoologically grouped between Ruminantia and other Artiodactyla. In p.146, it is seen that specimen, WRU, B 469 is in the same stage of epiphysial fusion as Hippopotamus amphibius (RS, floor) in Table No.54. Specimen, WRU, B467 (vide p. 147), however shows all the sluggish limb epiphyses fused except 10, 11 and 12. Ep.11 (proximal ulna) can be ignored as a traction epiphysis and of uncertain behaviour. Of the other two, the condition of fusion suggested distal ulna as the last to fuse. Thus it is also epiphysially intermediate between Ruminants and other Artiodactyls. To include this family into the average S.E.F. given above, the last line has to be written thus:-

4 (21,10 or 12)

The analysis shown in the foregoing pages has been done under the assumption that long bone epiphyses fuse in a constant sequence in animals belonging to the same species, varying little from genus to genus and, within small range, from family to family.

Todd and his co-workers had carried the investigation further and correlated them to the fusion of other epiphyses in the trunk and to eruption of teeth, closure of skull-sutures etc.. As the present study includes skeletons of animals showing different degrees of epiphysial fusion chiefly in the long bones with casual reference to tooth eruption and closure

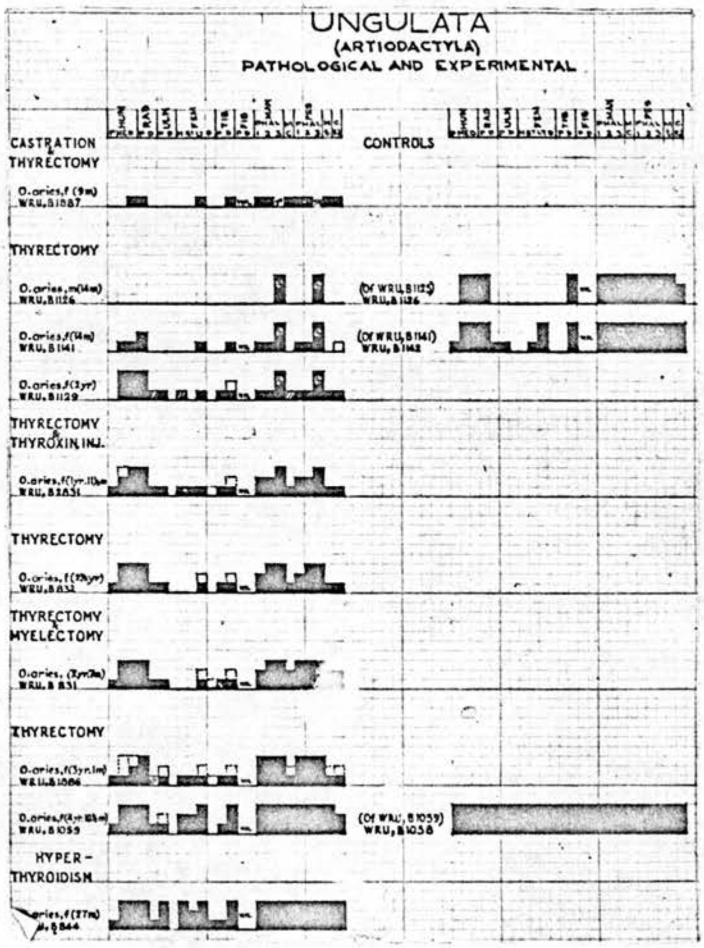


Fig. 41.

Epiphysial chart for the animals used by Simpson and Liddell at the Cornell University for experimental study of growth. Skeletal materials now housed at the Western Reserve University.

Ovis aries, WRU,B844 is an abnormal animal showing deficient growth in the skeleton probably due to hypothyroidism.

Abbreviations used are the same as in other charts.

of skull sutures, the sequence has to be worked out by a process of exclusion of common factors and by noting down the additional fusion of epiphyses in a series of skeletons of the same Species, Genus, Family, Suborder and Order arranged, not chronologically, but according to the maximum number of epiphyses fused or advancing towards fusion. It has thus been found possible to indicate the priority of fusion in cases where several epiphyses are seen fused in a skeleton. The attempt is perhaps hypothetical. But all workers (Donaldson[84], Dawson[28,77], Zuck[80], Koch[83], Todd[31] etc.) have realised that the first period of growth in most quadrupeds is very rapid and near its end is involved the closure of a large number of epiphyses in a short space of time. A blurred picture is given to the observer, just as in a Kinematographic film different poses run together to give an idea of action. The latter when slowed down would unfold the correct pose of the different units that make up the whole film. An experimental back ground to the conception of the sequence of epiphysial fusion may also be provided by slowing down the tempo of epiphysial fusion by surgical removal of some of those glands that control bone growth and at least the earlier part of epiphysial fusion. This was achieved by Simpson[44] and Liddell[43] through thyroidectomy, gonadectomy (vasectomy) and myelectomy on sheep of a constant breed at the Cornell University. In Tables Nos.60 and 61 and in Fig. 41, representing the Chart of Epiphysial Fusion

Table No. 60

A study of epiphysial union of Abnormal and Experimental Sheep (O.aries) bones in the W.R.U. Museum.

...rmality of ...ration	Hypothyroidism	Thyroidectomy				
...llected by	Todd	Simpson		Liddel		
...ber	B844	B1126	B1125	B1141	B1142	B1129
...	Female	Male	Male	Female	Female	Female
... at death	Abt.27mths.	14 mths.	14 mths. control of B 1126	14 mths.	14 mths. control of B 1141	2 years 1 mth.2days
" " opern.		1 mth.		1 mth.		
...ference		Q.J.Exp. Physiology 1924, 14, 181-185		Anat.Rec,1930, 30, 327 - 332		
EPIPHYSES						
Clav, St.....	absent					
Ac.....						
...m, Pr.El..	+	-	+	-	+	L.U.
" & Sh.	B	-	-	-	B	-
Di. El.	+	+	+	+	+	+
" & Sh.	+	-	+	B	+	+
Lat.Ep.	+	-	+	B	+	+
Med.Ep.	+	-	+	B	+	+
...d, Prox...	+	-	+	R	+	+
Dist...	B	-	-	-	B	- to B
...lna, Prox...	+	-	-	-	B	B
Dist...	-	-	-	-	-	-
...c, First..	absent					
Rest...	+	-	+	-	+	- to B
...(M), Prox...	+	-	+	B	+	B
Mid....	+	-	+	B	+	B
Term...	+	+	+	+	+	+
...n, Head...	+	-	-	-	-	- to B
Gr.Tr.	R	-	-	-	B	-
Ls.Tr.	+	-	ct.	B	+	B
Dist...	-	-	-	-	-	-
...b, Con....	B	-	-	-	-	B
Tb.....	-	-	-	B-	B-	-
Dist...	+	-	+	B	+	R
...b, Prox...	absent					
Dist...						
...lc. Epip...	+	-	R	B	+	B
..., First..	absent					
Rest...	+	-	+	-	+	B
...(P), Prox...	+	-	+	B	+	B
Mid....	+	-	+	B	+	B
Term...	+	+	+	+	+	+
...t. Centre..						
...L.FEATURE.		ep.8 unites with ep.5 & shaft hum.				
...BITS ETC.						
...MARKS	Maxill. development arrested at 11 mths. and upper facial at 24 mths. stage.					Phal. ep. partly L.U.
...TITION ...	M_1 stage M_2 erupting M_3 in crypt	M_1 stage M_2 erupting	M_2 stage M_3 crypt	M_1 stage M_2 erupting	M_2 stage M_3 crypt	M_2 stage M_3 crypt PM's imperfectly out.

Table No. 61

A study of epiphysial union of

Abnormal and Experimental Sheep (O.aries) bones in the W.R.U. Museum

lity n	Thyroidectomy				Thyroidectomy + castration	Thyroidectomy + myelectomy	Thyroidectomy + Thyroxin treatment
ed by	Simpson				Liddel	Simpson	
	B 832	B 1886	B 1059	B 1058	B 1887	B 831	B 2331
	Female	Female	Female	Female	Female		Female
death	2yrs.6m	3y.1m.6d	4y.10m.10d	4yr10m10d	8m.26d.	2y.6m.24d.	1y.10m.16d.
pern.	1mth.	1 mth.	1mth.3dys	control twin of B1059	2m.10d, castrn. shortly after	5m.12d, both operations	1m.12d, treatment CA.13d. after opern.
ce	Q.J.Exp.Phys,1924,14, 161	-		183	An. Rec, 1930,30	Q.J.Exp.Phys,1924,14	
	absent						
	B	B	B	+	-	L.U.	B
	B	B	B	+	-	B	B
	+	+	+	+	+	+	+
	+	R	+	+	B	+	R
	+	B	+	+	B	+	R
	+	B	+	+	B	+	R
	+	+	+	+	B	+	+
	B	B	B	+	-	B	B
	B	R	B	+	-	B	B
	-	-	-	+	-	-	-
	absent						
	B	B	+	+	B	R	B
	R	+	+	+	B	R	R
	+	+	+	+	B	+	R
	+	+	+	+	?	+	+
	-	B	R	+	-	-	B
	-	B	R	+	-	-	B
	R	B	+	+	B	B	B
	-	-	-	+	-	-	B
	B	B	B	+	-	B	B
	-	-	-	+	-	-	-
	B	B	+	+	B	B	B
	absent						
	B	B	R	+	-	R	B
	absent						
	B	B	+	+	B	R	B
	R	+	+	+	B	+	R
	+	+	+	+	h	+	R
	+	+	+	+	?	+	+
ATURE							
S		not well macerated			ungual phalanges covd. by hoof.	metatarsals & phalanges show signs of desease	thyroxin is unable to rectify earlier damage & retardation.
ION	M_2 stage M_3 crypt PM's imperfectly erupted.	M_2stage M_3crypt	M_2stage M_3 out	Standard much worn	M_1stage M_2crypt	skull M	M_1 stage M_2 out M_3 crypt

is is given an analysis of the same material now housed at the Hamann Museum, WRU, along with the skeleton of a sheep of retarded maturation and defective growth pattern due probably to hypothyroidism (WRU, B844,f). These operations succeeded, in addition to bony changes to be referred to later, in slowing down the velocity of epiphysial fusion to a remarkable degree, as compared with control animals and others of normal growth. For instance, the physical development of specimen, WRU, B1126,m operated at 1 month of age, was at about 3-month level when its control, aged 14 months, showed the normal epiphysial fusion. The sequence of fusion in these experimental and the retarded sheep as compared with normal sheep of various breeds is shown below:-

Experimental & abnormal sheep.	Normal Sheep of various breeds.
5	5,17,32
17,32	6 to 9,15,16,30,31
9	3
6,7,8,16,31	24
30	27
15	14,18,19,20,29
14,20,24,29	11
3	
27	
11,18	

It will be seen that the analytical study in the foregoing pages has also led to an average Artiodactyl pattern of S.E.F. that is even more spread out than and agrees very closely with the experimental findings as above.

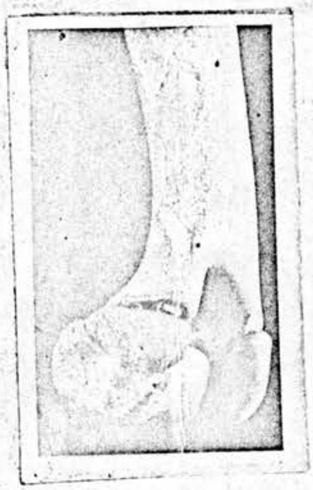


Fig. 42.

(from Todd and Todd[81])

Lower end of the left humerus of Ovis aries, male (WRU, B 1126), thyroidectomized. Physical development at about the 3-month level, though the chronological age is 14 months. Note union of lateral epicondyle with capitulum. Medial epicondyle is still ununited. All epiphyses at distal end of humerus are united in the normal twin of this animal, WRU, B 1125. (See pp. 288 &289 and Tables Nos. 97 & 98).

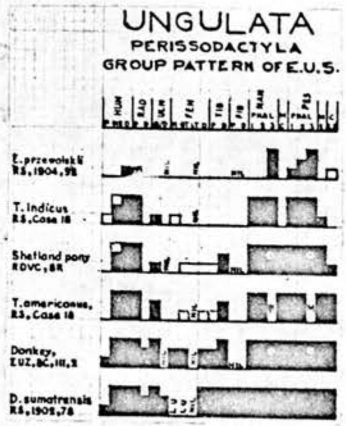


Fig. 43
Epiphysial chart
for Perissodactyla

Abbreviations same as in other charts. Dotted lines round a clear space indicates a stage which should have been attained. Full lines round a clear space indicates precocity. L.U. stands for lapsed union. A clear circular space with an asterisk or the letter G within indicates 'glazing' of the epiphysis.

The Epiphysis in Artiodactyla.

(a). Epiphyses at terminal phalanges were often absent as has been repeatedly shown in the foregoing pages. Radiographs of a new born camel (Fig.39) and a 16-day old antelope (Fig.4) do not show any epiphysial ossification at ungual phalanx though all the other phalanges are provided with such. In Tables Nos.54 to 61, the findings noted at terminal phalanges as "+" or "+ or nil" were actually cases where no sign of epiphysial ossification was observed. Out of 46 skeletons, that of a young pig only (RDVC,gal,6) showed definite presence of an epiphysis at 'R' stage of fusion. Where epiphyses were not found, the ends of ungual phalanges were seen to be lined with cartilage under cover of hoofs. Growth occurred in this cartilage from the adjacent shaft, as explained in page 17. Todd and Todd[81] however, hold that an epiphysis occurs in this situation and "union occurs simultaneously with ossification".

(b). The existence of 3 distinct centres of ossification in proximal humerus was seen in L.glama (Table No.54) and the new born camel (Fig.7).

(c). The epicondylar epiphyses lie dorsal to shaft of humerus specially in Pecora. The epiphysis for lateral epicondyle unites with distal epiphysis much earlier than with shaft of humerus; that for medial epicondyle unites with distal epiphysis after the latter has united with the shaft (Fig.42).

The Time Relation of Epiphysial Union in Artiodactyla.

It is apparent from what has been worked out in the previous pages that the pattern of epiphysial union is not related to growth or size. Koch from his large collection of materials of one race concludes that it is not a function of sex as well. An approximate pattern with minor variations is often evident in the same group of animals and seems to be the primitive characteristic for each group of mammals though the pattern is not necessarily the same for all mammals, as stressed by Stevenson (vide p.23).

Epiphysial maturation however runs independently of body maturation. The latter is associated with the velocity of growth which need not be the same as the velocity of epiphysial maturation or fusion. For instance, Todd and Todd[81] have shown that Ovis exhibits a well-marked acceleration over Bos in time - maturation relationships.

Tooth-Eruption Relationship to Epiphysial Pattern.

Such relationship is not constant. For instance, "in Sus and Capra, the third molar is erupted before union of distal humeral epiphysis. In Cervus, this approximately corresponds with union of distal tibial epiphysis. Bos seems to have similar relations as Cervus. In Ovis and antelopes, third molar erupts when femoral head fuses. Antilocapra, Camelus and Hippopotamus erupt third molars after fusion of the last long bone epiphysis, viz., proximal humerus. No zoological affinity is to be traced from the tooth eruption relationship to epiphysial pattern" (modified from Todd and Todd).

GENERAL OBSERVATIONS ON THE ARTIODACTYL PATTERN.

"Essentially, so far as the epiphysial union sequence goes, the order is uniform. Despite differences in shape of epiphyses and velocity in maturation, despite the differences in proportional growth between limbs and trunk no real differences in sequence are to be found" is what Todd and Todd[81] opined in their work on Ungulates. Koch[83] said "the sequence of epiphysial union is essentially the same in man, bison and the rat". The present study however differs from both these statements. A reference to the Epiphysial Charts shown in Figures, 36, 37, and 38 shows how limited is the application of this argument. No doubt the sequence pattern is uniform when members of Cervidae are considered amongst themselves, but amongst Suidae and Camelidae, Tragulidae and Giraffidae, the sequence differs considerably.

Three common features, however, are seen in the epiphysial fusion of Artiodactyls as given in the previous pages, viz.,

1). The terminal phalanges, when epiphysial, are the first to fuse.

2). The distal tibial epiphysis fuses earlier than that for metapodia.

3). Fusion of metapodial epiphysis is followed by that for proximal femur.

These three features may be utilized to divide the pattern of the sequence of epiphysial union in Artiodactyla into three stages.

Stage 1, involves the rapid closure of the following in succession.

Ungual phalanges
Proximal radius
Distal humerus
Middle and proximal phalanges, pes
Middle and proximal phalanges, manus
Humeral epicondyles
Distal tibia.

It is at this stage that 6 Artiodactyl specimens were found in the present study., viz., Pig No.18 of Prof.Brash, Camel (IM, m.g., 50), Deer (C.davidianus, RS,C15; O.virginianus, m, (WRU,B642), Shetland sheep (EUA) and Siberian ram (EUZ, BC,II,4). The epiphyses for humeral epicondyles are included in this stage. They follow or fuse simultaneously with the middle and proximal phalanges but precede distal tibia (Suidae, Giriffidae,Bovidae). They are immediately preceded by distal tibia in Cervidae (C.elaphus., EUA, floor; O.virginianus borealis, m, WRU, B642).

The fusion of these epiphyses enables the animal to give the required firmness to the arms and fulcra round those joints (toes, elbow and ankle) which are called upon to take the largest share in locomotion in proportion to their length, extent of articular surface and distance from the centre of the body.

This period may be considered as the juvenile period of the animal.

Stage 2, involves fusion of

Metatarsals
Metacarpals
Distal fibula
Head Femur
Trochanters of femur, Calcaneal epiphysis and proximal ulna.

The latter are placed at the end, since they are erratic and may fuse anywhere in this stage.

The completion of the first stage of fusion leaves the metapodia and femur free to grow and add to the length of the fore and hind limbs in a way that would increase the arms of the respective lever systems. This adds to the speed of the animal commensurate with the increase in length of its trunk. This stage was seen in Pig.No.19 of Prof.Brash, H.amphibius (RS,floor), D.aquaticus, m)WRU,B469), Ram (RDVC,gal,2), Soay sheep (EUZ, BC,II,4B & 4C), Ayrshire cow (RDVC,gal,I; the eps. for head and greater trochanter, femur was in 'R' stage). In Cervidae distal radius and ulna may be accelerated and fused before or along with proximal femur, (C.canadensis, WRU,B195, O.virginianus borealis,f,WRU,B648).

This period may be considered to be the puberty of the animal.

Stage 3, involves the fusion of the remaining epiphyses, viz

Distal radius, ulna and femur, and
Proximal tibia, fibula and humerus.

The animal enters upon its adolescence. Not much is henceforth added to the length of the limbs. The tempo of epiphysial activity has by this time slowed down. The epiphyses have now started uniting and it is a matter of opinion whether any of them would be considered as completely fused or in 'R' stage and would bring up the rear. Epiphysis for tibial tuberosity may be ignored.

Proximal humerus is usually the last to fuse (Rusa unicolor,m,IM,m.g.; Soay sheep, EUZ, BC,II,5, & 4A; O.aries, m,EUZ, gal; A.depressicornis, RS,1909, 43.1). Both Todd and Todd[81] and Koch[83] give the last position to this epiphysis. Distal femur has been seen to be the last to fuse in only one case (Camel RDVC,gal), where it was in 'R' stage. This may be taken as complete union, since the animal was a pretty old specimen with union of all skull sutures.

The epiphysial condition in Tragulus javanicus borneanus, m(WRU,B467) showed that distal radius and distal ulna would be the last two epiphyses to fuse in them. This animal is a great leaper and has very long hind limbs. Whether the fusional urge in the hind limbs is accelerated owing to their relatively greater need for being consolidated earlier than the forelimbs, and consequently the fusion in fore-limb epiphyses is retarded, is a question that cannot be decided on the findings on a single controverted (vide p.147) specimen.

The position of distal radial epiphysis in the fusion scale is ahead of distal ulnar, except in Caprinae (Black-faced

Table No.62

Approximate Order of Union of Epiphyses

In Artiodactyls: Present Work	In Artiodactyls: Todd & Todd[81]		In Bison (Koch[83])	In Rats (Todd[31]): Mus decumanus	In Rats (Todd[31]): Mus musculus	In Man (Todd[73])
Terminal phals.	Manus,pes	Phals.III	Dist.ep. &	Phal.III,	Phal.III,	Phal.II,III,pes
Dist.elem.,hum.	Humerus	med.epic.	epic.,hum.	manus & pes	manus & pes	Dist.ep.hum;
Prox.radius	Humerus	dist.ep.	Dist.tibia.	Phal.II,	Phal.II,	Lat.ep.hum.
Dist.ep.,hum.	Radius	head	Head rad;	manus & pes	manus & pes	
Middle phals.	Manus,pes	phals.II	Metacarps.;	Hum.Dist.	Phal.I,	Phal.III,manus;
Prox. phals.	Manus,pes	phals.I	Metatars.	Fem.,ls.troch.	manus & pes	Phal.I,pes;
Epic., hum.	Femur	ls.troch	Olecranon	Tib., dist.	Hum., dist.	Prox.radius &
Prox.el., hum.	Tib.,fib.	dist.	Head & gr.	Fib., dist.	Rad., prox.	ulna;calc.ep.
Distal tibia	Metacarpals		troch.fem.	Clav., lat.	Tib., dist.	Phal.II,I,manus;
	Metatarsals		Prox.tib.;	Phal.I,pes	Metacarpals	Med.epic.hum,
Metatarsals	Femur	gr.troch,	Dist.fem.	Fem., head	Metatarsals	Metatarsals.
Metacarpals;		& head.	Dist.rad.;	Metacarps;	Calc.ep.	
ls.troch.	Femur	distal	Dist.ulna	Metatars.	Fem.,ls.troch	Metacarpals,
Calc.epic.	Rad., ulna	distal	Prox.hum.	Hum.,med.ep.	Fem., head.	Dist.tib;
Prox. fem.;	Tib., fib.	prox.		Calc.ep.	Hum.,med.ep.	Dist.fib.
Dist.fib.	Humerus	prox.		Fem.,gr.troch.	Ulna, prox.	Femur,head &
Gr.trochanter				Clav.,st.end.	Fem.,gr.troch.	greater tro-
Prox. ulna				Fem., dist.	Fem., dist.	chanter.
				Rad., dist.	Hum., prox.	
Dist. rad.;				Ulna, dist.	Tib., prox.	Dist.femur;
Dist.ulna				Tib., prox.	Fib., prox.	Prox.tib. &
Dist.femur;				Hum., prox.	Rad., dist.	fib.
Prox.tib. &				Fib., prox.	Ulna, dist.	Dist.rad.& ulna
(Prox.fib.?)					Fib., dist.	
Prox. hum.(?)					Clavicle	Acrom.end,clav.
						Prox.hum.
						Stern.end,clav.

ewe, EUZ, BC,II,4B). Possibly they complete their fusion together (Shetland sheep EUZ, BC,II,5). Either or both of them, however, fuse earlier than distal femur and proximal tibia and fibula (C.canadensis, WRU, B195; O.virginianus borealis, WRU,B 648, the ewe and Shetland sheep mentioned before and A.depressicornis, RS,1909,43.1).

Of proximal fibula, sufficient material was not available for this study. Proximal tibia and distal femur, are seen to fuse together in Rusa unicolor, m, IM, m.g. & Soay sheep, f, (EUZ, BC,II,4).

In the following (Table No.62) is given the fusion sequence mostly followed in Artiodactyla. For comparison the sequence given by Todd and Todd for Artiodactyla and those given by Koch for the Bison and by Todd[31] for Mus decumanus and Mus musculus are shown.

A careful perusal of the Table (No.62) would show that Koch's statement is a sweeping generalization which cannot be accepted. Todd and Todd's statement, however, as far as the Artiodactyl is concerned is less dogmatic and more acceptable.

P E R I S S O D A C T Y L A.

"Odd-toed" unguligrade forms. Axis of limbs passes through middle of digit No.3, which is symmetrical in itself ('Mesaxonic' as opposed to the 'Paraxonic' limbs of Artiodactyls). Toes of hind foot are odd in number and are never more than three. Femur has a third trochanter. Fibula does not articulate with calcaneum and may, like ulna, be complete, or slender distally and incomplete. Pollex, hallux and digits 5 of pes are always absent.

Table No.63 gives a list of Perissodactyls studied.

Family TAPIRIDAE.

Medium sized animals. Manus with 4 digits, ulnar digit not reaching ground; pes with 3 digits; all hoofed. Ulna and fibula well-developed and s arate from radius and tibia.

3 young specimens and 1 adult (Tapirus indicus; IM,m.g) were studied. The young material (Table No.64) showed:-

In skel.	T. indicus, RS,C18		fusion of ep. 5,6,7,8,9, 15,16,17, 30,31,32
" "	WRU, B262, f	further	" " " 3,14,27,29 & impending fusion of ep24
" "	T.americanus,RS,C18	"	impending fusion of ep.24 & 11

TABLE No.63

List of Perissodactyl skeletons studied.

Family Genus etc.	Number of skeletons Total	 Young	 Adult	Habits, special features etc.
<u>Tapiridae</u>	4	3	1	Medium size; manus 4, pes 3 digits; ulna & fibula distinct and separate.
<u>Equidae</u>	19	9	10	Manus & pes 3- or 1-toed; ulna & fibula reduced & fused with radius and fibula.
<u>Equus</u>	14	7	7	Manus & pes with a single complete digit and proximal parts of metapodia 3 & 4
E. caballus	12	6	6	
E. prezwalskii	2	1	1	
<u>Asinus</u>	2	1	1	
Kiang	1	-	1	
Donkey	1	1	-	
<u>Hippotigris</u>	3	1	2	
E. burchelli	3	1	2	
<u>Rhinocerotidae</u>	4	1	3	Unwieldy size; ulna and fibula complete; radius 3 or 4, pes 3 digits ; digit 3 largest and symmetrical in itself.
Total	27	13	14	

Table No. 64

Order: UNGULATA Sub-order: Perissodactyla

S.Fam or Genus		Tapiridae		
		Tapirus		
Name	T.indicus	T.indicus	T.americanus	T.indicus
Museum Number	R.S. C.16	W.R.U. 2262	R.S. C.18	I.M. n.gal
Sex		Female		
Age				adult
EPIPHYSES				
Clav, St....	Never present			
Ac....				
Hum, Pr.El.	B	+	+	+
" & Sh.	B	-	-	+
Di.El.	+	+	+	+
" & Sh.	+	+	+	+
Int.Ep.	+	+	+	+
Med.Ep.	+	+	+	+
Rad, Prox..	+	+	+	+
Dist..	-	-	-	+
Ulna, Prox..	B	-	R	+
Dist..	-	B to -	-	+
Mc, First.	nil	nil	nil	nil
Rest..	-	+	+	+
Ph(M), Prox..	+	+	+	+
Mid...	+	+	+	+
Term..	+	+	M	+
Fem, Head..	B	-	-	+
Gr.Tr.	-	-	-	+
Ls.Tr.	ot.	-	-	+
Dist..	-	-	-	+
Tib, Con...	-	-	-	+
Tb....	-	-	-	+
Dist..	-	R	R	+
Fib, Prox..	-	-	-	+
Dist..	-	-	-	+
Calc. Epip..	-	+	+	+
Mt, First.	nil	nil	nil	nil
Rest..	- to B	+	+	+
Ph(P), Prox..	+	+	+	+
Mid...	+	+	+	+
Term..	+	+	M	+
Ext.Centre..				

SPL.FEATURE.

HABITS ETC..

REMARKS..... All toes touch the ground. Ulna transmits a third of the weight from humerus to wrist. Fibula is of no importance as a weight-transmitter.

	Early M_1 stage	M_1 stage	M_1 stage	
DENTITION...	M_1 erupting	M_2 & M_3 in crypt.	M_2 & M_3 in crypt	M_1 & M_2 out M_3 in crypt

Table No. 65

Order : UNGULATA Sub-order: Perissodactyla

E q u i d a e									Rhinocerotidae
E q u u s							Asinus		Dicerorhinus
Horse	Horse	Highland pony	E.Caballus	E.caballus (sh.pony)	E.caballus	E.przewalskii	Zebra-Horse hybrid	Donkey	R.Sumatranus
E.U.A. L31XIXa	E.U.A. L31XIXb	E.U.Z. BCIII5	E.U.A. L31XXI	R.D.V.C. B.R.	E.U.Z. L12425	R.S. 1904.92	E.U.Z. C.44	E.U.Z. B.C,III2	R.S. 1902.76
1 m. bef.full term birth	1 m.aft. birth	v.young	within 1 yr.aft.birth	1 yr. 7 m.		Male	new born		
N e v e r p r e s e n t.									
		-	x	+	+	x*	-	+	+
		-	x	-	B	x	-	B	B
		+	+	+	+	+	+	+	+
		-	B	+	R	B	-	+	+
		-	B	+	R	B	c.c.	+	+
		-	-	R	R	-	-	+	+
		-	B	+	R	B	-	+	+
		-	-	-	B	-	-	R	R
		-	-	B	B	-	-	+	+
		nil	nil	nil	nil	nil	nil	nil	R
nil	nil	nil	nil	nil	nil	nil	nil	nil	nil
-	-	-	+	+	+	-	-	+	+
-	-	-	+	+	+	-	-	+	+
-	-	-ct.	+	+	+	-	-	+	+
or nil	+ or nil	ct.	+	+ or nil	+?	+	+ or nil	+ or nil	+
		-		-	B	-	-	R	B(L.U
		-		B	E	-	-	R	-(L.U.)
		nil		B	ct.	nil	nil	nil	ct.
		-		B	B	-	-	R	+
		-		B	B	-	-	R	+
		-		-	-	-	-	R	R
		-		R	B	B	-	+	+
A B S E N T.									+
		-		B	B	B	-	+	+
nil	nil	nil	nil	nil	nil	nil	nil	nil	nil
-	-	-		+	R	-	-	+	+
-	-	-		+	+_	B	-	+	+
-	-	-		+	+	B(U), +(L)	-	+	+
or nil	+ or nil	ct.		+ or nil	+?	+	+ or nil	+ or nil	+
				$\frac{3,1,4,1}{3,1,3,1}$ M_2 erupting M_3 not in		$\frac{3,0,4,1}{3\ 0\ 4\ 1}$ or $\frac{2,0,4}{2\ 0\ 4}$		$\frac{3,1,4,3}{3\ 1\ 3\ 2}$ or M_3 or	M

i.e., the sequence is: All epiphyses at distal end and the fused epiphysis with shaft of humerus; all phalanges; proximal radius.
Elements of proximal humerus; metacarpals and metatarsals; calcaneal epiphysis.
Distal tibia, proximal ulna.

Family EQUIDAE.

Medium to large-sized animals; fast runners; ulna and fibula fused and reduced; manus and pes 3- or 1-toed, lateral digits being complete but functionless or reduced.

19 specimens were studied (Table No.63)

Genus Equus L.

Manus and pes have a single complete digit and proximal portions of metapodia 3 & 4 (splint bones).

14 skeletons of this genus were studied; of these 7 were adults. The younger specimens have been listed in Table No.65.

E. caballus.

12 skeletons studied. 6 of these were adults with limb ep. closed (a pony, EUA, L31, XV; a Shetland pony, EUA, central row; a Bay horse, m, WRU, B 852; an old horse, RDVC, gal, 3; E. caballus, WRU, Mr. Randall's collection; a Java mare, EUZ, BC, III, 2).

E. przewalskii.

2 skeletons studied; 1 of these was an adult mare (EUZ, BC, III, 5).

wear M_2 & M_3 cr

Sub-Genus Asinus.

2 specimens studied, 1 was an adult kiang (IM, m,g), the other a young donkey (Table No.65).

Sub-Genus Hippotigris.

3 specimens studied. 2 were adult, E. burchelli (RS, C14) and E. burchelli, m (WRU, B242). The young specimen was a new-born zebra-horse hybrid and is listed in Table No.65. It showed three distinct epiphysial centres in proximal humerus.

It was difficult to ascertain definitely whether the ungual phalanges had epiphyses. The writer has traced them in horses from immature condition (one month before full term and one month after birth, the skeletons being housed in EUA and described by Sir John Struthers[82]), very young condition after birth, within a year after birth (Sir John Struther collection), and at one year seven months (RDVC) to more mature condition when all the other phalanges had their epiphyses united, in new born zebra-horse hybrid and in adolescent donkey; but in none of them was an ungual ep. noticeable, though ep. for other phalanges were seen from specimens one month before birth. As in Ruminantia, the phalanges were lined with cartilage under cover of the hoof. Only in the przewalsky horse was there a very slight and doubtful sign of epiphysis.

Observation of the young Equidae material showed:-

In skel. Horse, EUA, L 31 XI, a & b fusion of ep. 17,32 (if non-appearance of ep. is to be regarded as fusion)

" " Highland pony, EUZ, BC III,5) and Zebra-horse hybrid, EUZ, C44) further fusion of ep.5

" " E. przewalskii, RS, 1904.92 " " of ep. 31

" " E. caballus, EUA, L31, XXI " " " ep. 14, 15,16 and presumably of ep. 31, since lower limb is not available and ep. 31 has showed signs of union in the foregoing specimen.

" " " " EUZ, LL24&25 further fusion of ep.3,30

" " Sh.pony, RDVC, BR " " " " 6,7, 9,29

" " Donkey, EUZ, BC, III,2 " " " " 8,24, 27

i.e., Terminal phalanges (if they have any epiphysis at all)

Distal elements humerus

Middle phalanx pes

Proximal and middle phalanges manus, metacarpals

Proximal phalanx pes, Proximal elements humerus

Lat. epicondyle and distal epiph. humerus, prox. radius, metatarsals.

Medial epicondyle humerus, calc. ep., distal tibia

<u>Family RHINOCEROTIDAE.</u>

Large unwieldy animals, ulna and fibula complete

wear M_2 & M_3 cr

and separate. Manus, 3 or 4 digits; pes, 3 digits; digit 3 larger than others and symmetrical in itself; digit 1 absent from manus and pes and digit 5 from pes; digit 5 when present in manus is smaller than others. Digits hoofed.

4 skeletons studied, 3 were adults, viz: R. unicornis (RS, gal, floor); R. unicornis, f (IM, m.g) and R. niger, f (IM, m.g). The only young specimen (Table No.65) showed fusion of ep. 3,5 to 9, 11,14 to 19 (18 & 19 showed 'lapsed union'), 21,22,24,25,36,27,29 to 32, clearly indicating that distal radius and distal ulna (now in 'R' stage) will follow, and proximal humerus (now in 'B' stage) will be the last to fuse.

The incidence of ep. fusion is represented below in symbols and as an epiphysial chart in Fig. 43.

Tapiridae.	Equidae.	Rhinocerotidae.
5 to 9,15,16,17,30, 31,32	17,32	3,5 to 9,11, 14 to 19 (20 nil), 21,22,23 (R), 24 to 27,29,30,31,32
	5	
3,14,27,29	31	
	14,15,16	
24,11		10,12 (presumptively)
	3,30	
		4 "
	6,7,9,29	
	8,24,27	

It is seen that fusion of ep. distal tibia follows that of eps. phalanges and eps. metapodia in Tapiridae and Equidae

wear M_2 & M_3cr

rather than the opposite, as occurs in all Artiodactyls. . What happens in the period corresponding to the second period of the latter when the femoral epiphyses should fuse, is not possible to ascertain in Tapiridae and Equidae owing to lack of adolescent material; but the single adolescent rhinoceros skeleton shows that the last portion of the third stage is finishing up lagging fusion in the fore-limb only, viz: in distal radius and ulna and in proximal humerus. One cannot generalize for the whole Sub-Order from one specimen only.

If the sequence in Rhinocerotidae is what prevails in the other families in the Perissodactyla, then the 3 stages of fusion in the two Sub-Orders would stand thus:

	Artiodactyla	Perissodactyla
Juvenility	Ungual phalanges	Ungual phalanges
	Proximal radius	Mid. phals., pes
	Distal humerus	Mid. & prox. phals., manus
	Mid. & prox. phal. pes	Prox. phals., pes
	" " " manus	Dist. ep., hum.; prox. radius
	Humeral epicondyles	Metacarps. & metatars.
	Distal tibia	Humeral epicondyles
		Distal tibia
Puberty	Metatarsals	
	Metacarpals	(Proximal femur)
	Prox. femur	
Adolescence	Dist. ulna & radius	(Distal femur, proximal tibia, prox. fibula)
	Dist. fem., prox. tib., prox. fibula	Distal ulna & radius
	Proximal humerus	Proximal humerus

wear M_2 & M_3 cr

<u>NOTE:</u> (1) Parantheses denote probability.

(2) Tragulidae & Camelidae differ from the above in the third stage of the schedule for Artiodactyls (see p. 146 & 147).

It will thus be seen that the above result disagrees with the statement of Todd & Todd that, in Perissodactyla "epiphysial sequence is precisely similar to that ...... of the Artiodactyla". Whether or not their assumption that "size, proportions of body and limbs and the differential of growths in limbs and trunk have no effect at all upon the sequence of union", can be accepted as such is beyond the range of criticism of the meagre Perissodactyl material available for this work.

The present work however shows clearly that the increase in length of metapodia in relation to increase in length of tibia is smaller in Perissodactyls than in Artiodactyls, since in the latter the metapodia gets a chance of growing for a much longer time. Hence, if not offset by increased growth in bones round other hind-limb joints or in advantageous adjustments between trunk and limb lengths, the Artiodactyla would theoretically be faster runners than Perissodactyla. The arrangement however is an improvement in Perissodactyls in the greater strengthening of their limb-bones in the juvenile period.

The present worker is not in a position to endorse or refute the statement of Todd & Todd that epiphysis for head femur is delayed to an unusual degree in Rhinoceros, since the only adolescent specimen that he could examine (Table No.65) had all limb epiphyses fused except those of distal radius and ulna and proximal humers. He has represented in page 174 the probable fusion by comparison with Equidae. Further, whether epiphyses for distal ulna and distal radius will invariably fuse before proximal humerus cannot be definitely stated on the observations on a single Rhinoceros.

<u>The Epiphysis in Perissodactyls.</u>

It is almost the same as in Artiodactyl.

(1) Tapiridae and Rhinocerotidae do have an ungual epiphysis. It is doubtful in przewalsky horse, but is universally absent in the horse, ass and zebra.

(2) The existence of 3 distinct centres of ossification in epiphysis for proximal humerus was distinctly seen in a zebra-horse hybrid (Table No.65).

(3) Epiphyses for lesser trochanter femur exist in the majority of the cases in Equidae and Rhinocerotidae as cartilage only. Ossification in them occurs from the shaft (see p. 17 & p.162).

(4) The third trochanter of femur was often provided with a separate epiphysis.

(5) A condition of 'lapsed union' (see p. 21) marked the epiphyses for greater and lesser trochanters in Rhinoceros sumatranus (RS, 1902.78).

(6) Similar epiphyses on opposite sides did not always present the same state of epiphysial activity.

A consideration of the S.E.F. of fast moving animals.

The Ungulata, the Carnivora and the Rodentia present some of the very swift mammals. Many of the ungulates possess great leaping powers in addition, though not to the same extent as the bigger carnivores. Below is shown the S.E.F. in such animals.

Ungulata		Carnivora		Rodentia	
Artiodactyla	Perissodactyla	Aeluroidea (Felidae)	Cynoidea	Simplicidentata	Duplicidentata
Term. phal. Prox.rad. Dist.hum. Other phals. Dist.tibia	Term.phal. Other phals. Di.hum;prox. rad;metatars.,metacarps Dist. tib.	Term.phal. Other phals; di. hum. Prox. rad. Metatars, metacarps Dist. tib. Dist. fib.	Term.phal. Dist.hum. Other phals; metatars; metacarps; pr.rad;hd. fem;di.ul. Di.tib.; di. fib.	Di.hum. Term.phal. Pr. rad. Other phals. Metatars; metacarps. Di. tib.; di. fib.	Di.hum; all phals pr. rad. metatars; metacarps Di.tib.; di. fib.
Metatars; metacarps Hd.fem.; dist.fib.	Hd. fem.	Hd. fem; prox.fib.	Prox. tib.; di. fem.; di. rad.	Head fem.	Head fem.
Dist.rad.; dist.ulna. Dist.fem.; prox. tib. Prox. hum.	Dist.fem; prox. tib; prox. fib. Dist. rad.; dist ulna Prox. hum.	Dist.fem. Prox.tib.; di. rad. Di. ulna Prox. hum.	Prox. fib. Prox. hum.	Prox.tib.; pr.fib. Di. fem. Di. rad.; di.ulna Pr. hum.	Di.fem.; pr.fib, di.rad; di.ulna Pr. tib. Pr. hum.

From the above it will be seen that in the juvenile period is included the fusion of epiphyses at the elbow, manus and pes of all swift animals except the Artiodactyla, in which the metapodial epiphyses continue growing and fuse during puberty along with epiphyses for proximal femur.

wear M_2 & M_3 cr

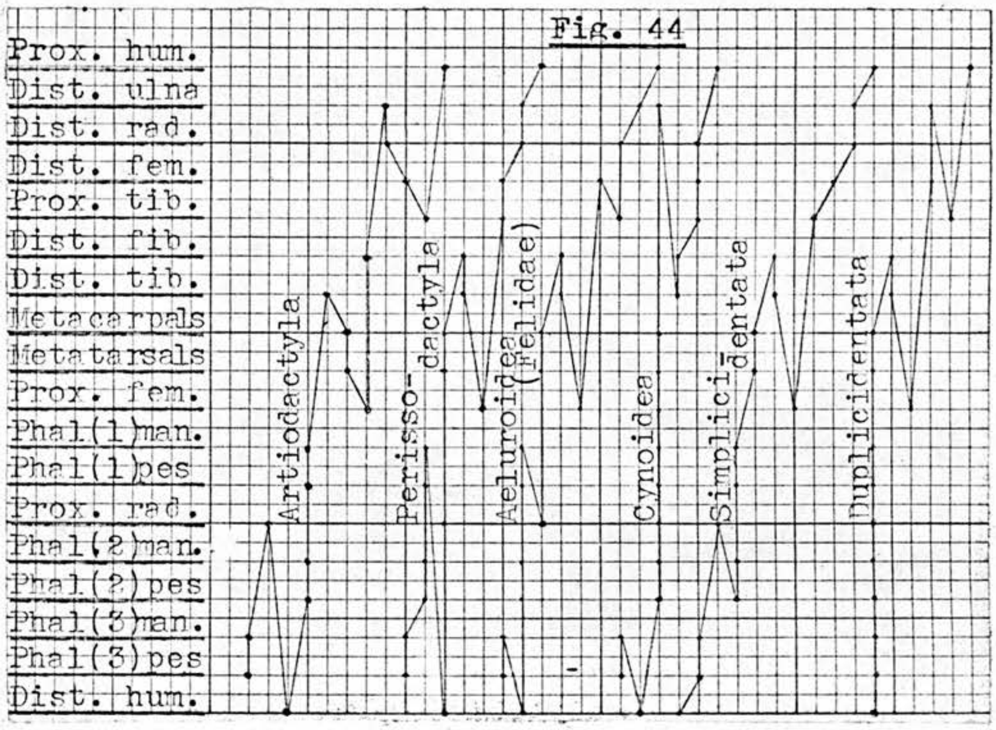


Fig. 44.

Graphs showing Convergence of the Sequences of Epiphysial Fusion in fast-moving animals.

wear M_2 & M_3 cr

Closure of proximal femoral epiphysis is preceded by distal radius and ulna in the deer (Cervidae) and precedes distal tibia and fibula in wolves, dogs and foxes (Cynoidea).

Epiphyses in the adolescent stage of swift animals close more or less in the same sequence. The proximal humerus always closes last and is immediately preceded usually by distal radius and ulna.

A graph is given below to show the condition as shown in the table in the previous page (Fig. 44).

Table No.66

Order: Hyracoidea Sub-order:

S.Fam or Genus	Procavia or Hyrax					
Name	H.cap-ensis	H.brucei	P.cap-ensis	P.lo-pesi	P.lo-pesi	P.cap-ensis
Museum Number	E.U.Z. ZL 1.2	I.M,m.g. 37	W.R.U. B 885	A.M.N.H 53793	A.M.N.H 53781	W.R.U. B694
Sex Age			Male young adult	Fem.	Fem.	Male adult
A.EPIPHYSES						
1.Clav, St....	Absent in Hyracoidea					
2. Ac....						
3.Hum, Pr.El.	+	+	+	+	+	+
4. " & Sh.	B-	-	B	B	B	B+
5. Di.El.	+	+	+	+	+	+
. " & Sh.	+	+	+	+	+	+
. Lat.Ep.	+	+	+	+	+	+
. Med.Ep.	R	R	+	+	+	+
.Rad, .Prox..	+	+	+	+	+	+
. Dist..	B	-	B	B	B	R
.Ulna, Prox..	B	R	+	+	+	+
. Dist..	B	-	B	B	B	R
.Mc, First.	vest	vest	vest	vest	vest	vest
. Rest..	B	-	+	B to R	B	+
.Ph(M),Prox..	B	B	+	+	+	+
. Mid...	B	+	+	+	+	+
. Term..	+	+	+	+	+	+
.Fem, Head..	B	B	M	R	+	+
. Gr.Tr.	B	B	B	+	R	+
. Ls.Tr.	nil	nil	+	+	+	+
. Dist..	B	B	B	B+	B	R
.Tib, Con...	B	-	B	B+	B	R
. Tb....	B	-	B	B	B	B+
. Dist..	B	-	+	+	+	+
.Fib, Prox..	B	-	B	B+	B	B+
. Dist..	B	-	+	+	+	+
.Calc. Epip..	B	+	+	+	+	+
.Mt, First.	nil	nil	nil	nil	nil	nil
. Rest..	B	-	+	+	B	+
.Ph(P),Prox..	B	B	+	+	R	+
. Mid...	B	+	+	+	+	+
. Term..	+	+	+	+	+	+
.Ext.Centre..						
.SPL.FEATURE.						
.HABITS ETC..	Live on rocky ground					
.REMARKS.....	Rock-Rabbit	Articulated skeleton				
DENTITION...	x	$\frac{1,0,43}{2\,0\,3\,3}$ slight wear	$\frac{1,0,4,3}{2\,0\,4\,1}$ M_3 or M_2 & M_3 cr	$\frac{1,0,4,3}{2,0\,4\,3}$	$\frac{1,0,4,3}{2\,0\,4\,3}$	$\frac{1,0,4,3}{2\,0\,4\,3}$

Table No. 67

Order:Hyracoidea Sub-order:

S.Fam or Genus	Dendrohyrax						
Name	P.emini	P.emini	P.emini	P.valida	P.valida	P.valida	P.valida
Museum Number	A.M.N.H 53321	A.M.N.H 53130	A.M.N.H 53314	W.R.U. B 1053	W.R.U. Box 1591 a	W.R.U. Box 1591 b	W.R.U. Box 1591 c
Sex	Male	Female	Female	Male			
Age							
A.EPIPHYSES							
1.Clav, St...	Absent in Hyracoidea						
2. Ac...							
3.Hum, Pr.El.	+	+	+	+			
4. " & Sh.	B	B	R	+			
5. Di.El.	+	+	+	+			
6. " & Sh.	+	+	+	+			
7. Lat.Ep.	+	+	+	+			
8. Med.Ep.	+	+	+	+			
9.Rad, Prox..	+	+	+	+			
10. Dist..	B	B	+	+			
11.Ulna, Prox..	+	+	+	+			
12. Dist..	B	B	+	+			
13.Mc, First.	vest	vest	vest	vest			
14. Rest..	B	+	+	+			
15.Ph(M), Prox..	B	+	+	+			
16. Mid...	R	+	+	+			
17. Term..	+	+	+	+			
18.Fem, Head..	+	+	+	+	+	+	+
19. Gr.Tr.	R	+	+	+	+	+	+
20. Ls.Tr.	+	+	+	+	+	+	+
21. Dist..	B	B	+	+	+	+	+
22.Tib, Con...	B	B	+	+	+	+	+
23. Tb....	B	B	+	+	+	+	+
24. Dist..	B	R	+	+	+	+	+
25.Fib, Prox..	B	B	+	+	+	+	+
26. Dist..	B	R	+	+	+	+	+
27.Calc. Epip..	N	+	+	+	+	+	+
28.Mt, First.	nil	nil	nil	nil	nil	nil	nil
29. Rest..	+	+	+	+	+	+	+
30.Ph(P), Prox..	B	+	+	+-	+	+	+
31. Mid...	B	+	+	+	+	+	+
32. Term..	B	+	+	+	+	+	+
33.Ext.Centre..							
B.SPL.FEATURE.							
C.HABITS ETC..	live on trees						
D.REMARKS.....					only hind limb bones available		
E.DENTITION... Skull M	1.0.4.3 / 2 0 4 3 $P \frac{1,2}{1,2}$ slight wear $M \frac{3}{3}$ No wear	1.0.4.3 / 2 0 4 3	1.0.4.3 / 2 0 4 3 slight wear				

THE STUDY OF EPIPHYSIS IN HYRACOIDEA.

Rodent-line plantigrade creatures of small size. Manus tetradactyle, pes tridactyle. Clavicles absent. Ulna and fibula complete. Os centrale present in carpus. Tail reduced.

The animals are not rodents and do not have characteristic ungulate features. Most of them live on rocky ground except the Dendrohyrax division which lives on trees.

6 specimens of Procavia (Table No.66) and 3 of Dendrohyrax (Table No.67) were available for study. Besides there were 2 adult specimens and 3 separate hind limbs of Dendrohyrax in which the epiphyses were closed. (WRU, B241; B1053,m; 3 right hind limbs without number in box No.1591).

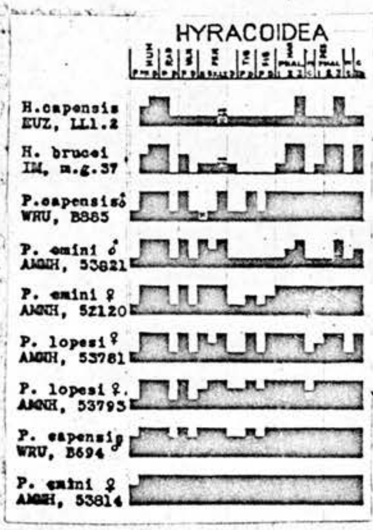
In Procavia the epiphyses were observed as follows:-

In skel.	EUZ,LL 1.2		fusion of ep.	3,5,6,7,9,17,32
" "	IM, m.g,37	further	" " "	16,27,31
" "	AMNH, 53791,f,	"	" " "	8,11,15,18,20,24,26
" "	WRU, B885,m,	"	" " "	14,29,30
" "	AMNH, 53793,f,) & WRU, B694,m)	"	" " "	19 (14 is 'B' to 'R' & 18 is 'R')

In Dendrohyrax, the epiphyses were observed as follows:-

In skel.	AMNH, 53821,m,		fusion of ep.	3,5 to 9,11,17,18, 20,29 (32 is 'B')
" "	" 52120,f,	further	" " "	14,15,16,19,27,30, 31,32
" "	" 53814,f	"	" " "	10,12,21 to 26
" "	WRU, B1053,m	"	" " "	4

Simplifying the above, the more important epiphyses may be put down as follows:-



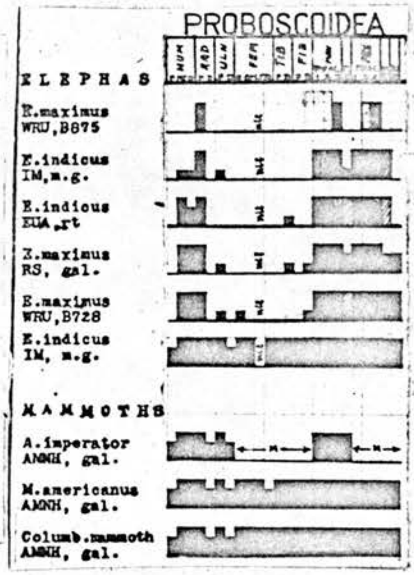


Fig. 45.
Epiphysial chart for Hyracoidea.

Fig. 46.
Epiphysial chart for Proboscidea. Epiphysial condition as observed in three skeletons of Mammoths is also shown.

Abbreviation in both graphs is the same. Hatching indicates a difference in epiphysial activity on the two sides or amongst different members on the same side. The phalanges and metapodia of elephants are seen to be in various grades of fusion. Glazing has been represented by clear circular areas with a central asterisk or the letter G. The circle has not come out well in the photograph.

Procavia	Dendrohyrax
Dist. ep. hum.(6); Lat. epic. hum (7); term. phals., manus & pes (17,32); prox. radius (9)	Dist. ep. hum.(6); lat. & epic. hum. (7,8); term. phal., manus (17); prox. rad. (9); metatarsals(29); head fem. (18)
Middle phals. manus & pes (16,31); calc. ep. (27)	Term. phals.,pes (32); mid. & prox. phals. manus & pes (15,16,30,31); calc. ep.(27) metacarpals (14)
Med. epic. hum.(8); prox. phal., manus (15); head femur(18); dist. tib. & fib.(24 & 26)	Dist. tib. & fib. (24,26); prox. tib. & fib. (22,25) dist. fem., rad. & ulna (21,10,12)
Prox. phal., pes (30); metatars.(29); metacarps(14)	Proximal humerus (4)

Comparing the type of fusion in Procavia during the period corresponding to juvenility and puberty in Artiodactyla, (see pp. 165 & 166) it is seen that it is different from the other types studied so far, in that fusion in phalangeal, metacarpal and metatarsal epiphyses is tardy in Procavia and is preceded by fusion of epiphyses round ankle and hip. In Dendrohyrax, however, the sequence falls more in line with that in generalised type of mammals e.g. the Centetidae. The sequences in the non-prehensile tailed Platyrrhines (Hapalidae and Nyctipithecinae) and in the Lemuroid (Lorisinae) in which the tarsals are not elongated, are a close approach to the sequence in Hyracoidea in that the acceleration in fusion of proximal femur and retardation in that of the phalanges are remarkably similar in all of them. (For Epiphysial Chart see Fig. 45).

Table No. 68

Order: **Proboscoidea** Sub-order:

.Fam

Genus **Elephas**

Name	Elephas maximus	Elephas indicus	Elephas indicus	Elephas maximus	Elephas maximus	Elephas indicus	Elephas indicus	Elephas indicus
Museum	W.R.U.	I.M,m.g.	E.U.A.	R.S,gal	W.R.U.	E.U.A.	I.M,m.g.	I.M,m.g.
Number	B875		Floor,rt	Floor	B728	floor,lt		
Sex	Male				Fem.			Male
Age	V.young (10 yrs)	Young	Young,				Adult	Old adult
EPIPHYSES								
Clav, St....	Absent in Proboscoidea							
Ac....								
Hum, Pr.El.	M	+	+	+	+	+	+	+
" & Sh.	-	-	-	-	-	-	R	+
Di.El.	+	+	+	+	+	+	+	+
" & Sh.	-	B	R	+	+	+	+	+
Lat.Ep.	-	B	-	+	+	+	+	+
Med.Ep.	-	R	+	+	+	+	+	+
Rad, Prox..	+	+	+	+	+	+	+	+
Dist..	-	-	-	-	-	-	+	+
Ulna, Prox..	-	B	-	B	B	B	+	+
Dist..	-	-	-	-	-	-	R	+
Mc, First.	x	R	+	+	?	+	+	+
Rest..	-	B	- to +	B to R	B to +	+	+	+
Ph(M), Prox..	-	+	+	+	+	+	+	+
Mid...	-	+	+	+	+	+	+	+
Term..	+	+	+ or nil	+	+ or nil	+ or nil	+	+
Fem, Head..	-	-	-	-	B	B	+	+
Gr.Tr.	-	-	-	-	-	B	+	+
Ls.Tr.	nil	nil	nil	nil	nil	nil	glazed	glazed
Dist..	-	-	-	-	-	-	+	+
Tib, Con...	-	-	-	-	-	-	+	+
Tb....	-	-	-	-	-	-	+	+
Dist..	-	B_	B	B	-	B	+	+
Fib, Prox..	-	-	-	-	-	-	+	+
Dist..	-	B_	-	B	B	B	+	+
Calc. Epip..	-	-	-	R	+	+	+	+
Mt, First.	x	M	+	+	?	+	+	+
Rest..	-	- to +	- to +	B to R	+	- to +	+	+
Ph(P), Prox..	-	+	+	+	+	+	+	+
Mid...	-	+	+	+	+	+	+	+
Term..	+	+	+ or nil	+	+ or nil	+ or nil	+	+
Ext.Centre..								
SPL.FEATURE.		at lower part of lateral supra-condylar ridge B						
HABITS ETC..								
REMARKS.....	legs not bent at elbow or knee but depend vertically from body.						old spec. lipping of articular surface	v.old sp. wide lipping
DENTITION...	1.0.1.1 / 1011	1.0.1.1 / 0011	1.0.1.1 / 0011	1.0.1.1 / 0011	1.0.0.1 / 1001	1.0.1.1 / 1011	1.0.0.1 / 0001	1.0.0.1 / 0001

Table No. 69

Order: Proboscoidea Sub-order: Mammoths

Mastodon

M.americanus A.M.N.H. Gallery	Columbian mammoth A.M.N.H. Gallery	Archidiskodon imperator A.M.N.H. Gallery
nil	nil	nil
nil	nil	nil
+	+	+
R	R	R
+	+	+
+	+	+
+	+	+
+	+	+
+	+	+
B+	B+	B+
+	+	+
B+	B+	B+
+	+	+
+	+	+
+	+	+
+	+	+
+	+	+
+	+	
+	+	
+	+	
R	+	
+	+	
+	+	
+	+	
+	+	
+	+	
+	+	
+	+	
+	+	
+	+	
+	+	
+	+	

fore-limb only available

THE STUDY OF EPIPHYSIS IN PROBOSCIDEA.

Large pachyderms. Digits five on both limbs. Legs not bent at elbow or knee in a position of rest as is seen in most quadrupeds, but depend vertically from the body. Walk with tips of toes on grounds, but weight of body carried by a cushion on posterior surface of digits; hence semiplantigrade. Radius fixed in prone position, crossing ulna. Femur without a third trochanter. Fibula articulates with calcaneum.

5 skeletons of Indian elephant, one of which was an adult (I.M., m, m.g) and 3 skeletons of African elephant were studied (Table No. 68) Prof. W. K. Gregory, at the instance of Prof. Brash, had kindly allowed the writer to study these specimens of Mammoths (2 Mastodons and 1 Archidiskodon) at the Gallery of the American Museum of Natural History (Table No. 69).

The epiphysial fusion of all these have been considered together as follows:-

In skel.	WRU, B875,m	fusion of ep.	5,9,17,32
" "	E. indicus, IM, m.g.,further	" " "	3,15,16, some 29,30,31
" "	EUA, floor, rt.	" " " "	8,13, some 14,28 some 29
" "	E. maximus, RS, gal.	" " " "	6, 7
" "	WRU, B723,f	" " " "	some 14,27 (13?,27?), 29 in all
" "	EUA, floor, lt.	" " " "	14 all(some 29 still'-')

In skel. M. americanus, AMNH, gal. further fusion of ep. 18,19, 20,22 to 26

" " Columbian Mammoth, AMNH, gal. further fusion of ep. 21

" " E. indicus, IM, m.g. " " " " 10,11 (ep. 20 glazed)

" " " " " ",m " " " " 12,4 (ep. 20 glazed)

The skeleton of Archidiskodon imperator (AMNH, gal) did not have a lower limb. In the fore-limb, the fusion was the same as in Columbian Mammoth.

Simplified, the fusion sequence may be reduced as:

Terminal phalanges, proximal radius
Other phalanges, some metatarsals
Med. epic. hum., some metatarsals & metacarpals
Distal epiph. hum. ; lat. epic. hum.
Some metacarpals, rest of metatarsals
Rest of metacarpals
Head and trochanters femur, distal tibia and fibula; proximal tibia and fibula
Distal femur
Proximal ulna and distal radius
Distal ulna and proximal femur

DISCUSSION:

The peculiarities in the epiphysial sequence chart (see Fig. 46) in this Order are,

(1) The early fusion of epiphysis for head radius.

(2) The fusion in epiphysis of metatarsals and metacarpals is a long drawn out process. It starts very early in the epiphysunion scale and continues till just before puberty, most of these epiphyses having united before distal

epiphysis humerus. This condition has been envisaged in the fusion scale of Equidae.

(3) There is a corresponding delay in fusion of the distal epiphysis of humerus. This condition has been foreshadowed in Perissodactyla, though its fusion occupies almost the first position in the scale of S.E.F. of most of the Orders studied before.

The reasons for this state of affairs may be two-fold:-

(1) The increasing and unwieldy weight of the animals of this Order makes it necessary that the feet should be consolidated as early as possible.

(2) "It is said that it hardly reaches proper maturity before forty"(Beddard). Hence the skeletons must have been obtained from animals of different ages in which successive stages of epiphysial fusion were spread out very considerably, instead of being hurried together in a short space of time as in animals of a much shorter span of life.

Regarding the difference, if there may be any, in epiphysial fusion in later periods, the only specimen supplying any clue is the Americam Mammoth (AMNH, gal) which showed an all round fusion of epiphyses from the late juvenile to the adolescent stage, viz., those round ankle, hip and knee, with the only exception of distal femur. But sufficient evidence is available to show that pressure at articular surfaces due to huge bulk or the conduction of this pressure along vertical limbs does not in any way affect the epiphysunion sequence in the late juvenile to adolescent periods of life. The present work agrees with the views of Todd and Todd as far as this stage is concerned.

Peculiarity noted in Proboscid limbs.

(1) As in most Perissodactyls, lesser trochanter femur presents no epiphysial centre for ossification. Glazing indicates completion of the process equivalent to fusion.

(2) Radius and ulna are crossed. Radius is very feeble and ulna is very much stouter than radius.

(3) First carpale and first tarsale are very long and project forward like a digit. Broom[71] has observed this elongation in the foot of the fossil Oudenodon of Anomodont genus. He considers that the first carpale or tarsale, in consideration of its length, may function as a digit. In that case, the first metacarpal or metatarsal with the epiphysis at the base would form the proximal phalanx and there would be the normal number of 3 phalanges in the thumb or big toe. The writer thinks it worthwhile tracing the centres of ossification in the first carpale and first tarsale. If these would show two centres of ossification, it stands to reason that one would represent the centre for the missing metacarpal which has been incorporated with the centre for the first carpale or tarsale.

TABLE NO.70
List of Edentata skeletons studied.

Sub-Orders Family Genus	Number of skeletons Total	Young	Adults	Habits, special features etc.
XENARTHA	33	21	12	Ischia united to sacrum.
Myrmecophagidae	16	11	5	Ant-eaters. Clavicles reduced, manus, digit 3 greatly developed, others reduced or absent. Pes, 4 or 5 subequal digits.
Myrmecophagus	7	3	4	Manus & pes pentadactyle.
Tamandua	7	6	1	Digit 5 of manus concealed
Cycloturus	2	2	-	Manus, 2 complete digits, (2 & 3). Pes, hallux concealed, other digits subequal. Clavicles complete.
Bradypodidae	4	2	2	Sloths. Vegetable-feeders Clavicles present; digits never more than 3.
Bradypus	3	2	1	3-toed sloth. Manus & pes with digits 2,3 & 4.
Choloepus	1	-	1	2-toed sloth. Manus, 2 digits. Pes,3 digits
Dasypodidae	13	8	5	Armadilloes; armour of bony scutes. Clavicles well-developed. Femur with third trochanter; tibia & fibula joined distally. Manus,4 or 5 digits. Pes, 5 digit plantigrade.
Dasypus	4	1	3	
Zaedyus or Chlamydophorus	2	2	-	
Priodontes	2	2	-	
Tolypeutes	2	1	1	
Smutsia	1	1	-	
Euphractus	1	1	-	
Tatusia	1	-	1	
NOMARTHA	7	3	4	Ischia not united to sacrum.
Manidae	5	2	3	Clavicles absent. Pentadactyle. Femur without 3rd troch.
Manis	5	2	3	
Orycteropodidae	2	1	1	Clavicles present. manus without pollex. Pes, 5 digits Femur with third trochanter.
Total	40	24	16	

Table No. 71

Order: EDENTATA Sub-order: Xenartha

S.Fam or Genus	Myrmecophagidae				
	Myrmecophagus			Cycloturus	
Name	Myrmecophagus tridactyla	Myrmecophagus tridactyla	Myrmecophagus tridactyla	Cycloturus didactylus	Cycloturus didactylus
Museum	F.M.	F.M.	F.M.	W.R.U.	W.R.U.
Number	49338	28310	20014	B 820	B1140
Sex	Female				
Age	young	young			
A.EPIPHYSES					
1.Clav, St....	rudimentary			M	+
2. Ac....					
3.Hum, Pr.El.	+	+	+	+	+
4. " & Sh.	B	B	B+	R	R
5. Di.El.	+	+	+	+	+
6. " & Sh.	B	B+	R	+	+
7. Lat.Ep.	B	B+	R	R	+
8. Med.Ep.	B	B+	R	B	+
9.Rad, Prox..	- to B	R	+	B	+
10. Dist..	do.	B+	R	B	+
11.Ulna, Prox..	B	R	R	B	+
12. Dist..	- to B	B	B+	B	+
13.Mc, First.	B	B	M	x	x
14. Rest..	B	B	M	+	+
15.Ph(M),Prox..	R to +	+	M	+	+
16. Mid...	do.	+	M	+	+
17. Term..	+	+	M	+	M
18.Fem, Head..	B	B	M	B	+
19. Gr.Tr.	B	B+	M	B	+
20. Ls.Tr.	-	nil	M	B	+
21. Dist..	B	B	M	B	B
22.Tib, Con...	B	B+	B+	B	B+
23. Tb....	B	B	B+	B	B+
24. Dist..	B	B	R	B	B+
25.Fib, Prox..	B	-	R	B	B+
26. Dist..	B	-	R	B	B+
27.Calc. Epip..	B	R	+	x	x
28.Mt, First.	B+	B	M	x	x
29. Rest..	B	B	M	+	+
30.Ph(P),Prox..	+	+	M	M	+
31. Mid...	+	+	M	M	+
32. Term..	+	+	M	M	+
33.Ext.Centre..					

B.SPL.FEATURE. gr. & ep. trochlea of hum. continuous — size of a rat

C.HABITS ETC.. terrestrial — arboreal

D.REMARKS.....

E.DENTITION... edentulous

Table No. 72

Order: EDENTATA Sub-order: Xenarthra

Fam.	M y r m e c o p h a g i d a e						B r a d y p o d i	
Genus	T a m a n d u a						B r a d y p u s	
Name	T. tetra-dactyla	T. tetra-dactyla mexicana	T. tetra-dactyla	T. tetra-dactyla instabilis	T. tetra-dactyla	T. tetra-dactyla mexicana	B. tridac-tylus	B. trida-tylus
Museum	W.R.U.	F.M.	W.R.U.	F.M.	F.M.	F.M.	W.R.U.	R.S.
Number	B883	22398	B277	18765	26562	22397	B 16	C.11
Sex		Female	Female	Female	Female	Male		
Age	young							
	r u d i m e n t a r y						nil	?
	+	+	+	M	+	+	-	+
	B	B	B	M	B+	R	-	R
	+	+	+	M	+	+	+	+
	B	B+	B	M	+	+	-	+
	nil	B+	B	M	+	+	ct.	+
	-	B+	B	M	+	+	-	+
	B	B	B	R	+	+	B	+
	B	B	B	B	B+	R	-	+
	B	B	B	B+	+	+	B	+
	B	B	B	B+	R	+	-	+
	B	M	+	+	M	+	x	+
	B	M	+	+	M	+	-	+
	+	M	+	+	M	+	-	+
	+	M	+	+	M	+	+	+
	+	M	+	+	M	+	+	+
	B	B	B	M	+	+	B	+
	B	B	B	M	+	+	B	+
	B	B	B	M	+	+	ct.	+
	B	B	B	M	B+	R	-	+
	B	B	R	B+	+	+	-	+
	B	B	B	B+	+	+	-	+
	B	B	B+	R+	+	+	-	+
	-	B	B	- to B	M	+	-	+
	B	B	B+	do.	M	+	-	+
	B	M	+	+	M	+	-	+
	B	M	+	+	M	+	x	+
	B	M	+	+	M	+	-	+
	R	M	+	+	M	+	-	+
	R	M	+	+	M	+	+	+
	+	M	+	+	M	+	+	+
	a r b o r e a l						2nd & 3rd phalanges fuse to form claw. a r b o r e a l	
	Smaller than Myrmecophaga. 3rd metacarpal very strong and has a strong claw.						Bases of metatarsals fused into a solid bl Ep.B continuous with trochlea.	
	E d e n t u l o u s						H o m o d o n t 5/4	

THE STUDY OF EPIPHYSIS IN EDENTATA.

Terrestrial, partly burrowing or arboreal creatures of quite small to gigantic size. Limbs clawed. Teeth absent or imperfect.

The Order is divided into two Divisions or Sub-Orders:-

1. Xenartha of New-World forms.
2. Nomartha or Old-World forms.

A list (Table No. 70) is given(p.185A) to show the skeletons studied under this Order.

Sub-Order XENARTHA:

Ischium united to sacrum.

Family MYRMECOPHAGIDAE:

Ant-eaters (Tables Nos. 71 & 72)

Clavicles reduced. In manus, digit 3 greatly developed and provided with a strong claw. In pes, 4 or 5 sub-equal digits with claws.

Myrmecophaga L. Long body. Terrestrial. Manus and pes, 5 digits. Walk on end of digit 5 and dorsal sides of digits 3 and 4 of manus and on sole of pes.

7 skeletons were availed for study at the Field Museum (FM) of Natural History, Chicago, U.S.A. Of these 4 were adults, viz., FM, 15966,26563,28309 and 49342. The remaining three showed :-

In skel. FM, 49338, f & FM, 28310		fusion of ep. 3,5,15,16,17, 30,31,32
" " FM, 20014	further	" " " 9 & 27

Tamandua - Smaller animals, arboreal. Manus, 5 digits, 5th concealed in skin; pes, 5 digits.

7 skeletons studied, of which Tamandua t.instabilis (FM,18835) was an adult. The epiphysial picture in the others was:-

In skel.	WRU, B883 & FM, 22398	fusion of ep.	3,5,15,16,17, 30 (R),31(R), 32
" "	WRU, B277 & FM, 18765	further " " "	13,14,27,28,29
" "	FM, 26562	" " " "	6,7,8,9,11,18,19, 20,22,23,24 (25, 26 M)
" "	FM, 22397	" " " "	12 (4,10 & 21 'R')
Presumably, last to fuse would be		"	4, 10 or 21

Cycloturus. Size of a rat. Arboreal. Manus - digits 2 and 3 complete, 4 has one nailless phalanx. Digits 1 and 5 consist of metacarpal only. Pes, hallux concealed, has one phalanx; digits 2 & 5 sub-equal. Clavicle complete.

Only 2 skeletons studied. They showed -

In skel.	WRU, B1140	fusion of ep.	3,5,6,14,15,16,17, 27,29 (phals. of pes missing)
" "	" B820	further " " "	7,8,9,10,11,12, 18,19,20 (30,31, 32)

Grafting the sequences in the 3 genera, the following S.E.F. is drawn up:-

Table No. 73

Order: EDENTATA Sub-order: Xenartha

Dasypodidae							
Euphractus	Zaedyus		Priodontes		Tolypeutes	Scutsia	Dasypus
Euphractus S.bolividae	Z.pichiy	Z.pichiy	P.giganteus	P.giganteus	Tolypeutes sp.	S.temminckii	Dasypus sp.
F.M.	F.M.	F.M.	R.S.	F.M.	F.M.	F.M.	K.U.A.
34347	25809	25617	1880,32.2	25271	28342	36582	L23XIV
Male young	Female			Female		Female	
M	A	x	nil	M	x	M	+
M	A	x	"	M	x	M	nil
+	+	+	+	+	+	+	+
B	-	B	B	R	R	R	+
+	+	+	+	+	+	+	+
B	R	+	+	+	+	+	+
B+	R	+	+	+	+	+	+
B+	R	+	+	+	+	+	+
R+	+	+	+	+	+	+	+
B	B	B	R	+	B	R	+
B	-	R	-	+	B	+	+
B	B	B	-	+	B	R	R
M	+	M	+	+	M	+	+
M	+	M	+	+	+	+	+
M	+	M	+	+	+	+	+
M	+	M	+	+	+	+	+
M	+	M	+	+	+	+	+
B	-	M	B	- to B	- to R	+	+
B	-	M	B	R	B+	R	+ or gl.
B	-	M	B	R	+ or nil	+	nil
B	-	M	-	B	B	B+	+
B	-	M	B	+	B	R	+
B	-	M	B	+	B	R	+
B	B	M	B	+	-	R	+
B	-	M	B	R	-	R	+
B	B	M	B	+	-	R	+
M	R	M	+	+	M	+	+
M	+	M	+	+	M	+	+
M	+	M	+	+	M	+	+
M	+	M	+	+	M	+	+
M	+	M	+	+	M	+	+
M	+	M	+	+	M	+	+
	glutgeal ep. B						
		Clavicles well developed					
Pig-like, omnivorous, nocturnal, burrowing							
Ep. 20 continuous with ep. 18			glutgeal ep. B; fem. articulates equally with tib. & fib.		artic.skel.	Ep.20 continuous with ep.18	delt. & ... glazed
		All homodont					
	8/9	8/9		18/18	9 or 8/9	x	9/M

3,5,15,16,17,32
30,31
27, (9 in Myrmecophagus)
13,14,28,29
6
7,8,9,11,18,19,20
(12,10, in Cycloturus).
22,23,24,26?
25,12
10,21,4

Family BRADYPODIDAE:

Sloths (Table No.72). Exclusively arboreal. Long anterior limbs, strong recurved claws; long bones without medullary cavities; clavicles present; digits never more than 3.

Bradypus L. - 3 toed sloth. Manus and pes, 3 digits (2, 3 & 4).

3 specimens studied: B.tridactylus (EUZ, 1939.25) was an adult. The others showed :-

In skel. WRU, B16 fusion of ep. 5,16,17,31,32
" " B.tridactylus (RS, C11) further fusion of ep. 3,6 to 15,18 to 30

Presumably, last to fuse would be ep. 4.

Choloepus L. - 2 toed sloth.

Manus - 2 digits (2 & 3)
Pes - 3 digits (2,3 & 4)

Only 1 adult skeleton (C. didactylus, WRU,B275) was available.

Family DASYPODIDAE:

Armadilloes (Table No.73). Pig-like. Fast runners, burrowers, nocturnal. Femur with a third trochanter. Tibia and fibula joined distally. Manus, 4 or 5 digits; strong curved claws. Pes, 5 digits; plantigrade.

13 skeletons were studied. Many were fragmentary; five were of adult animals (Dasypus sp., EUZ, BC, V.1; F.M. 28339; WRU, B276; D. sexcinctus, WRU, B276 & IM, s,m.gal. The others showed :-

In skel.	FM, 34347, m		fusion of ep.	3,5 (manus & pes 'M')
" "	FM, 23809, f	further	" " "	9,13 to 17, 28 to 32
" "	" 25617	"	" " "	6,7,8 (manus & lower limb 'M')
" "	RS, 1880,32.2	"	" " "	27
" "	FM, 28342	"	" " "	20
" "	FM, 36582, f	"	" " "	11,18
" "	FM, 25271, f	"	" " "	10,12(18 l.u. & 20 'R'),23, 24,26
" "	Dasypus, EUA, L23XIV	"	" " "	1,4,19,21,22, 25(12 is 'R')

Presumably last to fuse would be ep. 12.

Taking all the families together, the approximate order of union of epiphyses in Edentata is noted below (Epiphysial Chart in Fig.47).

3,5,15,16,17,32	i.e.	Elements of prox. & dist. ep. hum. term. phals., all; mid. & prox. phals., manus
30,31	"	Mid. & prox. phals., pes.
13,14,28,29	"	Metacarpals, metatarsals

27, (9)	i.e.	Calc. ep. (prox. rad. in Myrmecophagus & Dasypodidae)
6	"	Distal ep. humerus
7,8,9	"	Epiconds. hum.; prox. radius
(27)	"	(Calc. ep. in Dasypodidae)
11,18,19,20	"	Prox. ulna, head & troch. femur
(12, 10)	"	(Dist. rad. & ulna in Cyclo-turus & Dasypodidae)
24,26	"	Distal tibia and fibula
22,25	"	Prox. tibia and fibula
12	"	Distal ulna
10,21,(1,4)	"	Dist. rad., dist. fem., (st. ep. clav., & prox. hum. in Dasypodidae)
4, (12)	"	Prox. hum.; (dist. ulna in Dasypodidae)

NOTE: Figures and statements within parantheses indicate fusion etc. out of average schedule.

DISCUSSION:

While considering the S.E.F. in long bones of animals in this Sub-Order one should keep in mind the peculiar position of suspension from branches of trees in which many of them, the sloths in particular, pass all their lives, the recurved arrangement of their claws and the reduction in number and enlargement in size of their digits. Consequently, as distinguished from the arrangement in the Orders examined before, strain is taken away from the elbows and thrown on the manus and pes. Hence, the first to complete fusion are the phalanges followed by metacarpals and metatarsals and calcaneal epiphysis.

The maturation of epiphyses for distal humerus and proximal radius is retarded from a stage earlier than those of metacarpals and metatarsals to a later position in the fusion scale.

When the peculiarly arboreal and terresterial forms are considered the following modifications in manus and pes are found:-

1. Sloths have recurved claws in both manus and pes.

2. Ant-eaters have recurved claws in manus only.

3. Armadilloes do not have claws of fore-feet recurved. They have plantigrade pes.

In all of them the distal epiphysis of humerus matures later than metacarpals and metatarsals. In Myrmecophagus and Armadilloes, however, proximal radial epiphysis is trying to revert to its position, as in other mammals, of maturing close to the phalangeal epiphyses. In Armadilloes, the calcaneal epiphysis is pushed back near the position occupied in other mammals; and in Cycloturus and Armadilloes distal radial epiphysis is occupying a position similar to that in the fusion scale of Ungulates (Artiodactyla), viz., it closely follows fusion of epiphysis for head femur. Though the epiphysial evidence collected here is extremely meagre, the writer would timidly venture a suggestion that the limb-anatomy and habitat of the ancestral Edentate were sloth-like and induced major changes in the elbow-pedal epiphysial fusion relations. When the animals gave up their arboreal habit, the pes again assumed a plantigrade type and ultimately, in Armadilloes (notably in the 3-banded Armadillo), an almost digitigrade ungulate-like type; then epiphyses began to regress partially and show a vacillating picture between the pattern of S.E.F. in more normal terrestrial forms and that of the ancestral form. This suggestion is highly speculative and is open to modification, correction and even rejection. The palaeontological evidence, however, is encouraging. Ganodonta are allied to Edentata and, according to Beddard, represents the ancestral forms from which, at any rate, the Xenartha was derived. From the lowest Eocene strata, the Puerco beds of North America, has been found the earliest type of Ganodonta viz., the Hemiganus "the feet of which are specially comparable to the Ground Sloths". From the Upper Puerco (Torrejon) bed the remains of Psittacotherium have been found. Its foot offers "the most striking similarity" with that of the Ground Sloths. The foot of a still later form, coming from the Lower and Middle Eocene strata, the Stylinodon, is clearly like that of Psittacotherium.

Sub-Order NOMARTHA.

Ischia not united with sacrum.

Family Manidae.

Pangolins. Terrestrial and burrowing. Limbs short

Table No. 74

Order: EDENTATA Sub-order: Nomartha

M a n i d a e		Orycteropodidae
Manis		Orycteropodis
Manis	Manis pentadactyla	Orycteropodis afra
F.M.	B.U.Z.	R.S.
33550	KK19.3	1870,30.1
very young	adult	
nil	nil	nil
"	"	"
+	+	+
B	+	B
+	+	+
B	+	+
B	+	+
B	+	+
B	+	+
B	+	-
B	+	B
B	+	-
nil	nil	nil
M	+	+
M	+	+
M	+	+
M	+	+
- to B	+	-
B	R	B
-	+	B
-	+	-
-	+	B
-	+	B
-	+	R
-	+	B
-	+	R
B	+	+
M	+	+
M	+	+
M	+	+
M	+	+
M	+	+
		3rd trochanteric cp. in femur fibula articulates with femur
Ligamentous preparation		
Edentulous	Edentulous	Monodont 0,0,3,3 0 0 2 3

and carry 5 digits. Clavicle absent.

5 skeletons studied, of which 3 were adults, (Manis pentadactyla, EUZ, KK, 19.3; M. javanica, RS,C11; Manis f, FM, 46524). One was a very juvenile skeleton (M. macrura, WRU, B4) and had no value in epiphysial study. The only other specimen (Table No. 74) showed fusion of elements of the proximal and distal epiphyses of humerus; its manus and pes were missing.

Family ORYCTEROPODIDAE:

Burrowing. Clavicle, present. Manus without pollex; pes pentadactyle.

Only 2 specimens available of which one (O. capensis, EUZ, KK,20) was an adult. The other (Table No. 74) showed fusion of ep. 3,5,6,7,8,9,14 to 17,27 to 32, i.e., of all the elements of humerus distal ep. humerus, prox. radius, all epiphyses of manus and pes.

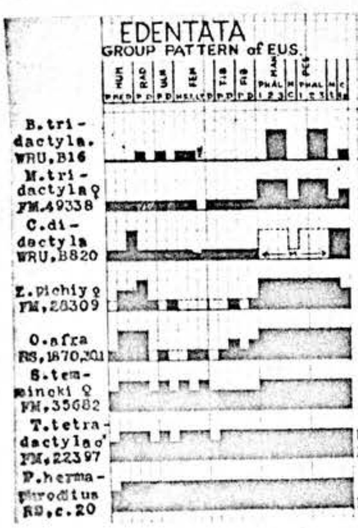
This again emphasises the need in burrowers of early maturation of articular ends at elbow, manus and pes.

Observations on the epiphyses of Edentata.

1. As in Orang (Figs. 8 & 8A) ep. medial epicondyle is continuous with trochlea.

2. Similar epiphyses of a series may not present the same stage of activity, e.g., in M. tridactyla, f, FM, 49338, ep. proximal radius and dist. ulna were in '-' stage on the left and 'B' on the right side; ep.

Fig. 47.



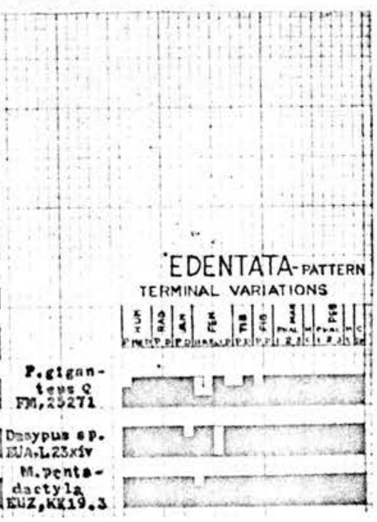


Fig. 48.

Fig. 49.

Epiphysial charts for Edentata.
Abbreviations as in other charts.

metacarpals 4 & 5 were in '-' stage on the left side whereas all others were in 'B' stage; of ep. for middle phalanges manus, that in digit 2 was in 'B' stage, in other digits they were in 'R' stage or closed; in P. giganteus, f, FM, 25271 and Tolypeutes sp., FM, 28342, ep. proximal femur was closed on one side but was wide open on the other.

3. Proximal fibula articulates with femur in Orycteropodidae.

4. 3 distinct elements were noticed in ep. prox. humerus (B. tridactylus, WRU, B16).

5. Lesser trochanter femur was often absent and was ossified from shaft (vide p. 17).

6. Failure of epiphysis to close and 'glazing' of sub-epiphysial surface to indicate completion of epiphysial activity explained in p.21 were seen in ep. greater trochanter femur (Dasypus sp., EUA, L 23 XIV), and in ep. lesser trochanter (O. capensis EUZ, KK,20).

7. Lapsed union was seen in head femur of Priodontes giganteus, f, FM, 25271.

Figure 48 represents an Epiphysial Chart showing the Pattern of Epiphysial Union in the whole Order (the "Group-pattern"). Figure 49 shows the "terminal" variations.

TABLE NO.75
List of Marsupialia skeletons studied.

Sub-Order Family Sub-Family Genus etc.	Number of skeletons Total	Young	Adults	Habits, special features etc.
DIPROTODONTIA	33	26	7	Two syndactylous toes.
Macropodidae	17	15	2	Hind limbs longer than fore.
Macropodinae	14	14	-	Kangaroos and wallabis.
Macropus	12	12	-	
Kangaroo	6	6	-	
Wallaby	6	6	-	
Petrogale	1	1	-	Rock kangaroo
Dendrolagus	1	1	-	Tree kangaroo
Potorinae	3	1	2	Rat kangaroo
Potorus	1	1	-	
Bettongia	2	-	2	
Phalangeridae	10	7	3	With parachute-like extension of skin.
Phalangerinae	9	6	3	
Petauroides	1	1	-	With flying membrane
Petaurus	1	1	-	" " ".
Trichosurus	4	2	2	
Phalanger	3	2	1	
Phascolarctinae	1	1	-	
Phascolarctus	1	1	-	Kaola. Good climber
Phascolomyidae	6	4	2	Fossorial
Phascolomys	6	4	2	Wombat
POLYPROTODONTIA	23	21	2	No syndactylism except in Peramalidae.
Peramelidae	2	2	-	Hind limbs longer than fore.
Perameles	1	1	-	Hallux present
Peragale	1	1	-	Hallux absent
Dasyuridae	13	12	1	Predatory, subequal limbs.
Thylacinus	3	2	1	Tasmanian wolf
Sarcophilus	6	6	-	Size of a badger
Dasyurus	2	2	-	Viverrine body
Antechinomys	1	1	-	Jerboa-like
Myrmecobius	1	1	-	Squirrel-like
Didelphyidae	8	7	1	Opossums
Didelphys	6	5	1	
Philander	2	2	-	
Total	56	47	9	

Table No. 76

Order MARSUPIALIA Sub-order: Diprotodontia Fam. Macropodidae

S.Fam or Genus	Macropodinae					
	Macropus					
Name	M.sp. (Kangaroo)	M.sp. (Kangaroo)	Micropus G.giganteus (Great Kangaroo)	Micropus G.giganteus	M.sp. (Kangaroo)	M.major (Gt.Kangaro
Museum	E.U.Z.	R.S.	A.M.N.H.	A.M.N.H.	E.U.A.	W.R.U.
Number	BC,VI2	1905,170.2	42904	42905	L23IV	B 727
Sex			Male	Female		Male
Age	juv.	juv.	young	adolescent	young	adult
A.EPIPHYSES						
1.Clav, St....	-	ct.	M	A	x	M
2. Ac....	nil	ct.	M	Q	x	M
3.Hum, Pr.El.	-	-	+	+	+	+
4. " & Sh.	-	-	-	B	-	B
5. Di.El.	+	+	+	+	+	+
6. " & Sh.	-	-	-	B	R	+
7. Lat.Ep.	-	-	-	B	B	+
8. Med.Ep.	-	-	-	-	B	+
9.Rad, Prox..	-	-	-	-	B	+
10. Dist..	-	-	-	B	-	B
11.Ulna, Prox..	-	B	B	B	B	+
12. Dist..	-	-	-	-	-	B
13.Mc, First.	-	-	R	R	?	+
14. Rest..	-	-	R	R	+	+
15.Ph(M), Prox..	-	-	+	+	+	+
16. Mid...	-	-	+	+	+	+
17. Term.	+ or nil	+	+	+	+	+
18.Fem, Head..	-	-	-	B	B_-	B
19. Gr.Tr.	-	-	B	B	B	B
20. Ls.Tr.	ct.	nil	nil	nil	B	+
21. Dist..	-	-	B	B	-	+
22.Tib, Con...	-	-	-	-	B_-	B
23. Tb....	-	-	-	-	B_-	B
24. Dist..	-	-	B	B	B_+	-
25.Fib, Prox..	-	-	-	-	B_-	-
26. Dist..	-	-	-	B	B_+	-
27.Calc. Epip..	-	B	R	+	+	+
28.Mt, First.	nil	nil	nil	nil	nil	nil
29. Rest..	-	-	R	+	+	+
30.Ph(P), Prox..	-	-	+	+	+	+
31. Mid...	-	-	+	+	+	+
32. Term..	+ or nil	+	+	+	+	+
33.Ext.Centre..						
B.SPL.FEATURE.		styloid ulna artic. with ulnare	Massive crest of tibia			
C.HABITS ETC..		Kangaroo is terrestrial and deer-like				
D.REMARKS.....		ulna forms ¼th surface for wrist joint				
	$\frac{3.0.2.2}{1\ 0\ 2\ 2}$ M_3 erupt-ing	$\frac{3.0.2.2}{1\ 0\ 2\ 2}$ M_3 erupt-ing	M	M	$\frac{3.0.2.2}{1\ 0\ 2\ 2}$	$\frac{3.0.1.2}{1\ 0\ 2\ 2}$ M_3 erupting

Table No. 77

Order: MARSUPIALIA Sub-Order: Diprotodontia Fam: Macropodidae

Fam.	Macropodinae								Potoroinae
us	Macropus								Potorus
e	M.bennetti (Wallaby)	M.bennetti	M.ualabatus (Wallaby)	M.bruni	Wallaby	Wallaby	P.xanthopus (Rock wallaby)	D.inustus (tree kangaroo)	P.tridactyla
eum	R.S.	W.R.U.	E.U.Z.	W.R.U.	R.D.V.C	R.D.V.C	W.R.U.	W.R.U.	W.R.U.
ber	1936,2	B 182	BC,VI,2	B1350	B.R.	B.R.	B 192	B 193	B 191
			Female		Male	Female			
	young	young	young	young	young	young	immature	immature	adolesc
	x	-	?	B	M	M	A	M	?
	x	ct.	?	ct.	M	M	A	M	?
	B	-	+	-	+	+	B	+	+
	-	-	-	-	B	B	B	-	B
	+	+	+	+	+	+	B+	+	?
	-	B	-	B	B+	B	B	B	?
	-	B	-	B	R	B	B	B	?
	-	-	-	B	B	B	B	B	?
	-	B	B	B	-	B	B-	B	+
	-	-	-	-	-	B	-	-	B
	-	B	B	B	B	B	B	R	+
	-	-	-	-	-	B	-	-	B
	-	-	B	B	+	+	B	+	?
	ct.	-	B	R	B	B	B	+	?
	ct.	B	B	+	+	+	B	+	?
	ct.	B ?	B	+	+	+	B	+	?
	-	+ ?	+	+	+	+	+ or nil	+	?
	-	B	B	B+	B	B	B	+	?
	-	B	B-	B	-	B	B	B	B
	-	B	-	B	-	B	ct.	B	B
	-	-	-	B	B	B	B	B	B
	-	-	-	B	-	B	-	-	B
	-	-	-	B	-	-	-	-	?
	-	B	-	B	B	B	B	B	B
	-	-	-	-	-	-	B	-	B
	-	B	B	B	-	B	B	B	B
	-	-	B-	B	B	R	B ?	+	?
	nil	nil	nil	nil	nil	nil	Rud	Rud	nil
	-	-	B	R	B to R	- to R	B	+	?
	-	-	+	+	+	+	B	+	?
	-	B	+	+	+	+	B	+	?
	-	+ ?	+	+	+	+	+ or nil	+	?
			delt. ep. in ct.						
	t.2to4 have ep. at each end	3 distinct elem. in ep. 3		3 dist. elem. in ep. 3			3 dist. elem. in ep. 3		
	considerable leaping powers					delt.ep. ossified	rock dwellers	arboreal	
			loose ep. glued, ep. study ?				tib. fb. is a distinct ep.	ep.8 continuous with troch.	
	3,0,2,1	3,0,2,4	3,0,1,4	3,0,1,4	3,0,1,4	3,0,1,4	3,0,2,3	2,0,2,4	3,C,2,4
	1,0,2,1	1,0,2,4	1,0,1,4	1,0,1,4	1,0,1,4	1,0,1,4	1,0,2,3	1,0,1,4	1,0,1,4
			no wear	no wear			M_4crypt no wear		

THE STUDY OF EPIPHYSIS IN MARSUPIALIA.

Terrestrial, arboreal or burrowing (rarely aquatic). Clavicle developed. Bones of forearm separate. 5 digits in manus (except in Choeropus). Fibula free. Usually 5 digits in hind limb (hallux often absent).

It is divided into two Sub-Orders - (Table No.75).

1. Diprotodontia
2. Polyprotodontia

D I P R O T O D O N T I A.

Two syndactylous toes, except in Caenolestes.

Family MACROPODIDAE.

Terrestrial, rarely arboreal; saltatorial; deer-like habits. Hind limbs longer than fore. Pes syndactylous, 4 digits, hallux absent, 4th toe very large.

Sub-Family Macropodinae.

Kangaroos and wallabies. Size from that of a rabbit to that of a man.

The study consisted of 6 skeletons of kangaroo, 6 of wallaby, 1 rock-wallaby and 1 tree kangaroo(Tables Nos.76 & 77). The epiphysial fusion was as follows :-

Kangaroo.

In Macropus sp.,EUZ,BC,VI,2,fusion of ep. 5,17?,32?(no sign of ep. in 17 & 32; noted as fused).

Table No.78 .

Order: MARSUPIALIA Sub-Order: Diprotodontia Fam: Phalangeridae

Fam.	Phalangerinae						Phascolarctinae
	Petauroides	Petaurus	Trichosurus		Phalanger		Phascolarctus
	P.volans	P.breviceps	T.vulpecula	T.vulpecula	P.ursinus	P.maculatus	Phascolarctus (kaola)
	E.U.Z.	W.R.U.	E.U.Z.	W.R.U.	A.M.N.H.	F.M.	A.M.N.H
	BC,VI,2	B 187	BC,VI,2	B 188	30596	31752	42903
					Male	Male	Male
	juv.	y.adult	y.adult	adult	young	young	young
	A	B	x	+	M	A	A
	A	B	x	+	M	A	A
	+	+	+	+	R	+	+
	-	B	R	R	B	B	B+
	+	+	+	+	-	+	+
	-	+	+	+	E	B	B+
	-	+	+	+	B	B	R
	-	+	+	+	-	B	R
	-	+	+	+	M	B+	B
	-	B	-	R	M	B	-
	B	+	+	+	M	B+	B
	-	B	-	R	M	B	-
	R	+	+	+	M	B	B
	R	+	+	+	M	B	B
	+	+	+	+	M	B	+
	+	+	+	+	M	B	+
	+	+	+ or nil	+	M	M	+
	-	- to B	R ?	+	+	B	B
	-	- to B	R ?	+	R	B	B
	ct.	B	R ?	+	+	B	B
	-	B	R	+	B	B	B
	-	B	B ?	+	M	- to B	B
	-	B	B ?	+	M	- to B	B
	-	B	+	+	M	B+	R
	-	B	R	+	M	B	B
	-	- to B	+	+	M	B+	R
	+	+	+	+	M	x	-
	+	+	+	+	M	B	B
	+	+	+	+	M	B	B
	+	+	+	+	M	B	+
	+	+	+	+	M	B	+
	+	+	+ or nil	+	M	M	+
						ep.8 unites with trochlea	
	arboreal						
	ligamentous sp.		ligamentous sp.				ligamentous sp.
	3.1.2.4 / 1 0 1 4	3.1.3.4 / 2 0 3 4	3.1.2.3 / 1 0 2 3	3.1.2.4 / 1 0 1 4	2.1.2.4 / 2 1 1 4	x	x
		slight wear			incisors only worn		

Family PHALANGERIDAE.

Arboreal, parachute-like expansions for flying leaps.

5 fingers and toes, pes syndactylous.

Sub-Family Phalangerinae.

Tail generally prehensile.

Genus Petauroides.

With flying membrane. 1 skeleton examined. (Table No. 78)

In P.volans,EUZ,BC,VI,2 fusion of ep. 3,5,13 to 17,
27 to 32.

NOTE. Ep.13,14,28,29, though included in the above were just short of fusion. Fusion shown in the above specimen may be split up into 3,5,15,16,17,27,30,31,32, and 13,14, 28,29 .

Genus Petaurus.

With flying membrane. Medium or small size.

1 skeleton examined (Table No. 78).

In P.breviceps, WRU,B187, fusion of ep. 3,5,13 to 17,
27 to 32,
and 6,7,8,9,11.

Genus Trichosurus.

Large size. Flying membrane less marked.

4 skeletons examined, 2 being adult (T.vulpecula, EUZ,BC,VI,2 and WRU,B1359,m). The others (Table No. 78) showed -

In EUZ,BC,VI, 2 fusion of ep.3,5 to 9,11,13 to 16,
17?,24,26,27 to 31,
32? (? indicates no sign of ep.).

" WRU,B188 further " " " 1,2,18 to 23,25.

Hence, fusion was still held over in ep. 4,10,12.

Genus Phalanger.

Large size. 3 specimens studied, 1 being adult (P. latus, FM, 31750), in which all epiphyses including those at both ends of clavicle were fused. The others (Table No. 78) showed -

In P. ursinus, m, AMNH, 30596 fusion of ep. 18 & 20 (dist. eps. hum. were '-' or 'B' and forearms, legs, manus and pes missing)

" P. maculatus, m, FM, 31752 further fusion of ep. 3,5 (term. phals. missing, rest 'B' or '-')

Assuming that terminal phalanges, if present, were fused, this genus presents a condition unprecedented so far in that proximal femur is united even before fusion of phalanges and epiphyses of humerus. But this has occurred in only one specimen, the other (FM, 31752) showing a more advanced condition of fusion in ep. 3 & 5 while 18 & 20 were only 'B'.

As compared with Macropodinae, the general order of fusion in the Phalangerinae, except the genus Phalanger, may be represented thus -

5	i.e.	elements of distal humerus
17,32	"	terminal phalanges
3	"	elements of proximal humerus
15,16,30,31,27	"	proximal and middle phalanges, manus & pes; calcaneal epiphysis

13,14,28,29	i.e.	metacarpals and metatarsals
6,7,8,9,11	"	epiconds. and dist. ep. hum.; prox. rad. and ulna
24,26	"	distal tibia and fibula
18 to 23, 25	"	proximal eps. femur, tibia & fibula; dist. fem.
4,10,12	"	proximal humerus; distal radius & ulna

In genus Phalanger, however, it is -

3,5,17?,32?	i.e.	proximal and distal elements hum.; term. phals.
18,20	"	head and lesser trochanter femur

Sub-Family PHASCOLARCTINAE.

Genus Phascolarctus.

Kaola. A good climber.

In specimen, AMNH, 42903, m (Table No. 78) there was fusion of ep. 3,5,15,16,17, 30,31

Hence it presents no difference from Phalangerinae in general, as fas as the above epiphyses are concerned.

Family PHASCOLOMYIDAE.

Fossorial. Limbs subequal; manus with 5 subequal digits; pes with 4 strong toes and a short hallux, digits 2 and 3 have a tendency to syndactylism.

Genus Phascolomys.

Wombat. Partially webbed feet, hence as aquatic as beaver.

6 skeletons studied; 2 were adults with clavicular epiphyses fused (P. tasmanianus, WRU, B886; P. talifrons, RS, C10, which showed a special ossicle connected by

Table No. 79

Order: MARSUPIALIA Sub-order: Diprotodontia

Fa.	P h a s c o l o m y i d a e				
nus	P h a s c o l o m y s				
me	P. ursinus	P. tasmanianus	P. tasmanianus	P. talifrons	P. talifrons
seum mber x ge	E.U.Z. RH 53	W.R.U. B 183 Male young	W.R.U. B 601	W.R.U. B 602	R. S. C.10
	-	A	A	A	Q
	nil	ct.	A	?	Q
	R	+	+	rt. B lt. +	+
	B	B	B	rt. - lt. +	+
	+	+	+	rt. + lt. +	+
	B	B	B	rt. B lt. +	+
	B	B	B	rt. B lt. +	+
	B	B	B	rt. R lt. +	+
	B	B	- to B	+	+
	-	-	B	+	+
	B	B	- to B	+	+
	-	-	B	+	+
	-	B	+	+	+
	B	B	+	+	+
	B	B	+	+	+
	B	B	+	+	+
	+ or nil	+	+	+	+
	B	B	B	B	+
	B	B	- to B	B	+
	B	B	-	R	+
	-	M	- to B	-	+
	-	B	B	-	+
	R	B	B	-	+
	B	B	B	-	+
	-	B	B	-	+
	B	B	B	-	+
	B	M	+	+	+
	-	B	+	+	+
	B	B	+	+	+
	-	B	+	+	+
	-	B	+	+	+
	+ or nil	+	+	+	+ fabella
	separate OS trigonum		strong lat. epicondylar crest in humerus		lat. condyle femur articulates with fibula

Fossorial, root-eating forms, limbs sub-equal, incisors rodent-like and powerful. Partially webbed hind foot, i.e, aquatic, beaver-like. Heavy body, short legs, therefore not very active; trudges along with a heavy rolling waddle. Burrows v. deep.

	ligamentous sp.			
1.0.1.4 / 1 0 1 4	1.0.1.4 / 1 0 1 4 highly worn	1.0.1.4 / 1 0 1 4 very much worn M_4 carious	1.0.1.4 / 1 0 1 4	1.0.1.4 / 1 0 1 4

ligaments with postero-superior angle of proximal end of fibula - Fabella?).

The others (Table No. 79) showed -

In P. ursinus, EUZ,HH,53		fusion of ep. 5,17?,32? (? indicates non-existence)
" P. tasmanianus, m,WRU,B183		further fusion of ep. 3
" " "	" B601	" " " 13 to 16, 27 to 31
" " "	" B602	" " " 4,6,7,8 (these eps. were less advanced on the right side), 9,11, 10,12

Hence fusion was still held over in ep. 18 to 26, i.e. all eps. femur, tibia and fibula (whole hind limb)

Therefore the approximate order of fusion is -

5,	i.e.	elements of distal humerus
17,32	"	terminal phalanges
3	"	elements of proximal humerus
15,16,30,31,27, 13,14,28,29	"	middle & prox. phals. manus & pes; calc. ep.; metatars. & metacarps.
6,7,8,9,11,10, 12,4	"	epicond. & dist. ep. hum.; prox. rad. & ulna; prox. hum.; dist. rad. & ulna

DISCUSSION:

Crafting the sequences in Macropodidae, Phalangeridae and Phascolomyidae an approximate order of union may be drawn as follows: -

Distal elements humerus (ep. 5)
Terminal phalanges, manus & pes (eps. 17 &32)
Proximal elements humerus (ep. 3)
Middle & proximal phalanges, pes (eps. 31,30)
Middle & proximal phalanges, manus (eps. 16,15)
Calc. epiph.; metatarsals; lat. ep. clav. (eps. 27, 28,29,2)

Metacarpals (eps. 13,14); (prox. femur, ep.18, in tree-kangaroo)
Dist. epiph. & epic. humerus; prox. radius & ulna (eps. 6,7,8,9,11)
(Lesser trochanter & dist. ep. femur in kangaroo; ep. 20 & 21)

Distal tibia & fibula (eps. 24 & 26)
Head, trochanters & distal ep. femur (eps. 18,19, 20,21)
Proximal tibia (eps. 22 & 23)
Proximal fibula (ep. 25)
Distal radius & ulna; proximal humerus (eps. 10,12 & 4)

The above schedule seems to be applicable, with one exception, to every Diprodont up to the fusion of the epiphyses at elbow, viz, those at distal humerus and proximal radius and ulna. It implies the need for early consolidation of all epiphyses of manus and pes together with those at elbow. The end of this period may be compared to that seen in Ungulata (pp.165 & 166) and termed the 'juvenile' period for this Sub-Order. It differs from the Ungulata in that it excludes distal tibia and fibula and includes the metatarsals and metacarpals. Compared to Cervidae (kangaroos have been termed 'marsupial-deer'), in which distal tibia (fibula absent) fuses earlier than metapodia, it is seen that progression involves a different principle in the deer, since their fore and hind limbs do not differ in length so enormously as in the kangaroo. Consequently, their distal tibia (ankle) has the same urge as the elbow (distal humerus, proximal radius and proximal ulna) and unites early, leaving the metapodia to continue their growth into the stage of 'puberty' (p.166). In kangaroo, however, the hind limbs must grow longer. Increase in length in metatarsals will not help it in growing taller in height, since, unlike the deer and ruminants, it rests on its whole pes. Addition to the length of bone of thigh and leg is the only way of increasing the length of the hind limbs. Distal tibia is therefore exempted from early fusion. This hypothesis may explain why metapodia should fuse so early in kangaroos, earlier even than distal epiphysis humerus - a phenomenon not met with in this study, except in the arboreal Insectivores (Tupaia, p.52) and to a certain extent in the volant Galeopithecidae (p. 56).

Two questions may arise in this connection. First, why metacarpals should have the same fate as metatarsals, which alone have the macropodiform modification? Probably the 'gene' for metapodia are similar and modification in the one affects the other as well. Secondly why the same condition should occur in Diprotodonts having no macropodiform modification? Probably kangaroo has handed down the ancestral form of Diprotodonts. Later adaptations have modified the shape and size of the bones but have not occurred sufficiently long to affect the 'gene' for epiphysial fusion.

In the case of the exception mentioned above, a single Phalanger ursinus, AMNH, 30596, early fusion of proximal femur was found. This was not however found in an almost similar animal, P. maculatus, FM,31752. More observation is necessary to understand the principle involved in such cases.

The epiphyses to fuse next seem to follow at least two slightly different schedules:-

(1) Approximately as in the generalised type of mammals. Such is seen in Phalangeridae and, it is inferred, in Macropodidae. It presents fusion, in the period corresponding to the puberty of Ungulates (p. 166), of:-

Distal tibia and fibula (eps. 24 & 26)
Proximal & distal epiphyses of femur (eps. 18,19, 20,21)

Kangaroos differ from the above in that distal epiphysis and lesser trochanter of femur unite earlier than distal tibia, distal fibula and head and greater trochanter of femur (eps. 24,26,18 & 19).

In this portion of fusion, there is a resemblance with what occurs in the Ungulates, except that distal femur is reserved for fusion in the period corresponding to the adolescent stage of Ungulates (pp. 166,167).

In this stage ('adolescent stage'), the fusion can be represented as follows:-

Proximal tibia (eps. 22, 23)
Proximal fibula (ep. 25)
Distal radius, distal ulna & proximal humerus (ep. 10, 12 & 4)

In Ungulates this stage icludes distal femur as well.

(2) In Phascolomyidae, the fusion is peculiar and seems to be linked with the individual limbs.

In '<u>puberty</u>', <u>fore-limb</u> epiphyses that missed fusion in the previous or 'juvenile' period close up fusion. These are:-

Distal radius & ulna; proximal humerus
(eps. 10, 12 & 4)

<u>In 'adolescence'</u>, <u>hind-limb</u> epiphyses that did not fuse in the 'juvenile' period come up to complete the fusion-list. These are:-

Proximal & distal femur, tibia & fibula
(eps. 24,26,18,19,20,21,22,23,25)

Whether any of eps. 24,26 and 18 (19 & 20) may fuse before the others and thus should be included in 'puberty' is a possibility that could not be studied on the limited material available. Even assuming that this had happened, the point in the early and simultaneous fusion of distal radius and ulna and of proximal humerus is peculiar and cannot be ignored.

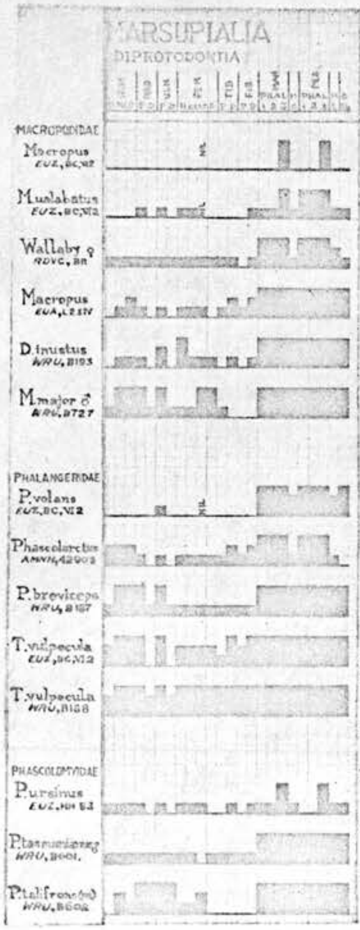
<u>Epiphysial Peculiarity in Diprotodontia.</u>

(1) Terminal phalangeal units were often non-epiphysial.

(2) Metatarsals may have epiphysis at both ends (RS, 1936,2).

(3) Three distinct elements in proximal epiphysis of humerus were seen in Macropus, EUZ, BC, VI,2; Wallaby,

upper M° 8



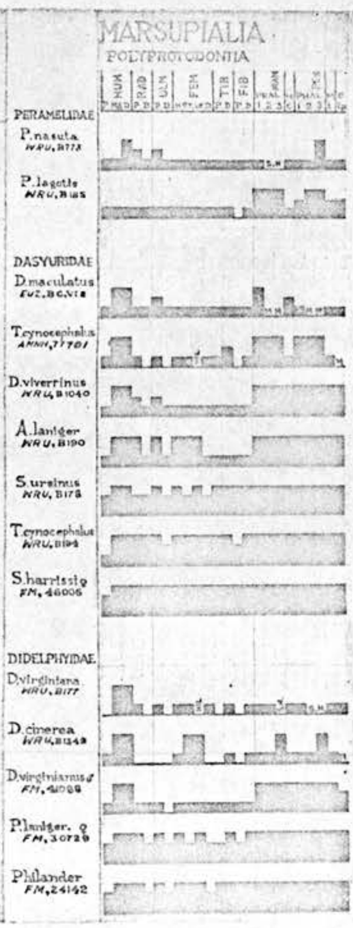
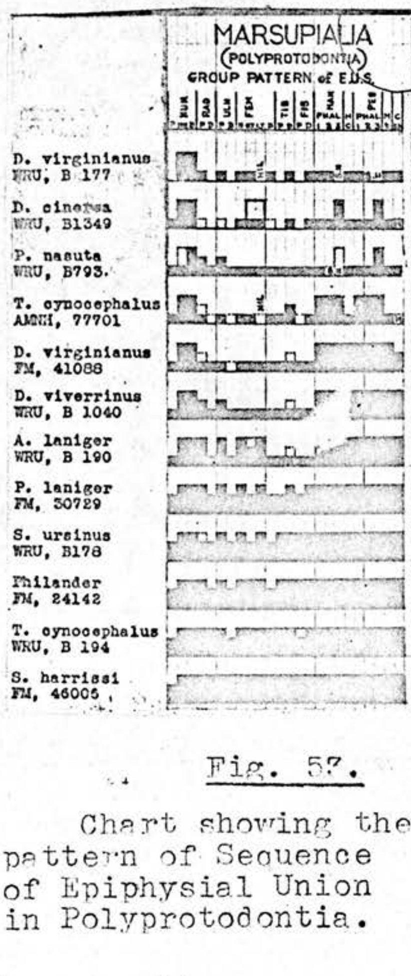


Fig. 50 Fig. 51

Epiphysial charts for Diprotodontia and Polyprotodontia. Abbreviations same as in other charts.



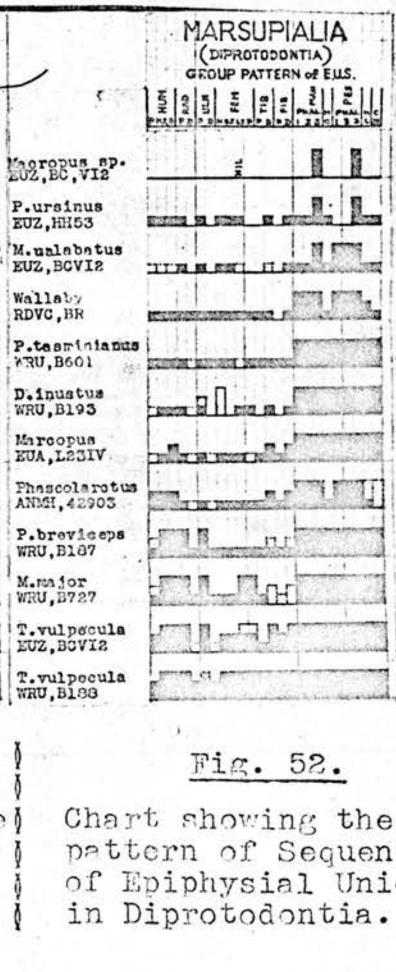


Fig. 57.

Chart showing the pattern of Sequence of Epiphysial Union in Polyprotodontia.

Fig. 52.

Chart showing the pattern of Sequence of Epiphysial Union in Diprotodontia.

WRU, B182, & B1350; and Petrogale xanthopus, WRU, B192.

(4) Tubercle of tibia presented a massive crest in kangaroos. Spec. WRU,B193 showed a distinct ep. for it.

(5) Deltoid tuberosity in humerus bore an epiphysis in Wallaby, f (RDVC, BR) and was ossified.

(6) Fabella was present in one specimen (Phascolomys talifrons, RS, C10).

(7) Both medial and lateral epicondyles were united to trochlea and capitellum as well as to shaft of humerus in a few specimens (Dendrolagus inustus, WRU, B193; Petauroides volans, EUZ, BC, VI,2; Phalanger maculatus, m, FM, 31752; Phascolomys tasmanianus, WRU, B183 and P. talifrons, WRU, B602).

Epiphysis Chart (Fig. 50) and Group Pattern of E.U.S. (Fig. 52) are annexed.

P O L Y P R O T O D O N T I A.

Without syndactylism except in Peramelidae.

Family PERAMELIDAE:

Bandicoots. Fossorial. Clavicle absent. Hind legs longer than fore. Digits pentadactyle. Digits 2 and e of pes syndactylous and slender; hallux small or absent. Manus with 2 or 3 of middle digits functional, others small or absent.

Genus Peragale.

Rabbit bandicoots. Hallux absent.

uppos H'S

Table No.80

Order: MARSUPIALIA Sub-order: Polyprotodontia

D a s y u r i d a e

Thylacinus			Sarcophilus					
T.cyno-cephalus	T.cyno-cephalus	T.cyno-cephalus	S.ursi-nus	S.ursi-nus	S.ursi-nus	S.ursi-nus	S.har-rissi	S.har-rissi
A.M.N.H	A.M.N.H	A.M.N.H	E.U.Z.	W.R.U.	R.S.	W.R.U.	F.M.	F.M.
77701	B194	35244	HH47.3	B238	1884,32.1	B178	46006	46028
		Male					Female	
young	y.adult.	adult	young	young	adult		adult	adult
M	M	M	ct.	M	Gl.	M	Q	M
M	M	M	nil	M	Gl.	M..	Q	M
+	+	+	+	+	+	+	+	+
B	B	+	-	B	B	B+	R	R
+	+	+	+	+	+	+	+	+
+	+	+	R	R	+	+	+	+
+	+	+	R	B	+	+	+	+
+	+	+	B	B	+	+	+	+
B	+	+	B	B	+	+	+	+
-	+	+	B	B	+	+	+	+
B	+	+	B	R	+	+	+	+
-	R	+	B	B	R	R	+	+
B	+	+	+	+	+	+	+	+
B	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+
+	+	+	+	+	+	+	+	+
- to B	+	+	B	B	R	+	+	+
do	+	+	B	B	R	R	+	+
nil	+	+	-	B	R	+	+	+
- to B	+	+	-	B	R	R	+	+
B	+	+	-	B	+	+	+	M
B	+	+	B	B	+	+	+	M
B+	+	+	B	R	+	+	+	M
nil	R	+	-	B	+	+	+	M
B	+	+	B	B	+	+	+	M
M	+	+	+	+	+	+	+	+
nil.	nil	nil	nil	nil	nil	nil	nil	nil
B	+	+	R	R to +	+	+	+	+
+	+	+	R	+	+	+	+	+
+	+	+	R	+	+	+	+	+
+	+	+	+	+	+	+	+	+

Ferocious, nocturnal, burrower, predatory, carnivorous, without hallux

standard	standard	standard	4,1,2,4 / 4 1 2 4	4,1,2,4 / 3 1 2 4 much worn tartar on upper M's	4,1,2,3 / 3 1 2 3	4,1,2,4 / 3 1 2 4	4,1,2,4, / 3 1 3 3 much worn	4,1,3,3 / 2 1 3 3 much w[illegible] many absorb[illegible]

One skeleton studied (Table No.81).

P. lagotis, WRU, B185 showed fusion of ep. 5,15, 16,17, 30 ('R'), 31,32. (Medial epicondyle continuous with trochlea).

Genus Perameles.

Hallux present.

One skeleton studied (Table No.81).

P. nasuata, WRU, B773, showed fusion of ep. 3,5,6, 17?, 32 (ep. 16 & 17 were ligament covered and could not be studied well).

Family DASYURIDAE:

Predatory, usually pentadactyle, hallux may be absent.

Genus Thylacinus.

Tasmanian wolf, hallux absent.

3 skeletons studied (Table No. 80).

T. Cynocephalus, AMNH, 77701, showed fusion of ep. 3,5,6,7,8,15,16,17,30,31,32.

" WRU, B194 showed further fusion of ep. 9,10,11,13,14,18,19,20,21,22, 23,24,26,27,29

" m, AMNH,35244 showed further fusion of ep. 12,23 & 4 (clavicles 'M')

Genus Sarcophilus.

Size of a badger. Hallux absent.

6 skeletons of Sarcophilus ursinus studied (Table No. 80).

Table No. 81

Order: MARSUPIALIA Sub-order: Polyprotodontia

D a s y u	r i d	a e		P e r a m e l i d a e	
Dasyurus		Antechinomys	Myrmecobius	Peragale	Perameles
D.maculatus	D.viverrinus	A.laniger	M.fasciatus	Peragale lagotis	Perameles nasuta
L. U. Z.	W. R. U.	W.R.U.	W. R. U.	W.R.U.	W.R.U.
BC,VI, 2	B 1040	B 190	B 546	B 185	B 773
Female					
Young	Young	Young		Young	Y.adult
nil	ct.	?	M	M	M
"	+	?	M	M	M
+	+	+	+	B	+
B	B	B	B	B	B
+	+	+	+	+	+
+	+	+	+	B_	+
+	+	+	+	B	B
+	+	+	+	B	B
B	R	+	+	B	R
B	B	B	B	B	B
R	R	+	+	B	R
B	B	B	B	B	B
B	+	+ ?	+	B	B
R	+	+ ?	+	B	B
+	+	+ ?	+	+	B
M	+	+ ?	+	+	?
M	+	+ ?	+	+	?
B	B	+	M	B	B
B	B	+	M	B	B
B	B	+	M	B	B
B	B	B	M	B	B
B	B	B	M	B	B
-	B	B	M	B	B
B	B	B	M	B	B
B	B	B	M	-	B
B	B	B	M	B	B
B	+	+	M	B+	B ?
B	+	nil	M	nil	B
B	+	⊕ ?	M	R to B	B
B	+	+ ?	M	R	B
M	+	+ ?	M	+	B
M	+	+ ?	M	+	+
dealt op. ossified			hum. very strong and square shaped	hind legs longer than fore. Pes digits 2 & 3, syndactylous	
	body viverrine, nocturnal, insectivorous	jerboa-like, terrestrial		fossorial, insectivorous	
ligamentous sp., op. readings ?	union of op. at wrist just begun	v. delicate & tiny sp., op. readings of manus & pes ?		these have the most well developed patella amongst all marsupials	
M	4.1.2.4 3 1 2 4 not much worn	4.1.3.4 3 1 3 4	M	4.1.3.4 3 1 3 4	5.1.3.4 3 1 3 4 slight wear

In skel.	EUZ, HH, 47.3	fusion of eps.	3,5,13,14,15,16,17, 27,32
" "	WRU, B238	further " " "	30,31,29 (some)
" "	RS, 1884, 32.1	" " " "	6,7,8,9,10,11,22,23, 24,25,26, remaining 29
" "	WRU, B178.	" " " "	18,20
" "	F.M, 46006,f) & F,M. 46028)	" " " "	12,19,21

Hence last to fuse would be ep. 4

Genus Dasyurus:

Body viverrine. Hallux may be absent.

2 skeletons examined (Table No.81).

D. maculatus, f, EUZ,BC,VI 2 showed fusion of eps. 3,5,6,7, 8,15 (16,17,31 & 32 were missing)

D. viverrinus,f, WRU,B1040 " fusion of eps. 3,5,6,7, 8,13,14,15,16,17,27, 28,29,30,31,32 (9 & 11 were 'R')

Genus Phascologale:

Almost the size of a rat; hallux present.

P. flaviceps, WRU, B189 was the only specimen available for study. The skeleton was fragmentary and covered by dried ligaments. Hence hot studied for epiphysial fusion.

Genus Antechinomys.

Jerboa-like, terrestrial, without hallux. (Table No.81).

A laniger WRU, B190 showed fusion of eps. 3,5,6,7,8,9,11, (13,14,15,16,17,ligamentous),18,19,20,27,28,29,(30,31,32 ligamentous).

Table No.82

Order: MARSUPIALIA Sub-order: Polyprotodontia

...s.	Didelphyidae						
...nus	Didelphys					Philander	
...ies	D.virginianus	D.virginianus	D.virginianus	D.cinerea	D.virginianus	P.laniger derbianus	Philander sp.
...seum	F.M.	F.M.	W.R.U.	W.R.U.	F.M.	F.M.	F.M.
...mber	47601	D.D.D's	B 177	B 1349	41088	30729	24142
...x	Female	Male			Male	Female	
...e	juv.	juv.	young	young	young	y.adult	adult
	M	M	M	x	M	R	x
	M	M	M	x	M	+	?
	sep.	x	+	+	+	+	+
	-	x	-	B	B	B_+	R
	+	x	+	+	+	+	+
	B	x	+	+	+	+	+
	-	x	+	+	+	+	+
	B	x	+	+	+	+	+
	B	B	B	-	B	+	+
	-	-	-	-	B	R	R
	B	B	B	-	B	+	+
	-	-	-	-	-	R	R
	-	B	B	B	R	+	M
	-	B	B	B to -	B_+ to +	+	M
	B	M	B	B	R to +	+	M
	M	M	B	B	+	+	M
	M	M	?	+ ?	+	+	M
	B	B	B	B	B	+	+
	B	B	B	+	B	R	+
	B	B	ct.	+	B	+	+
	-	-	B	-	B	B_+	R
	-	-	-	-	B	R	R
	-	-	-	-	B	R	R
	-	B	B	B	B	+	+
	-	-	-	-	B	B_+	R
	B	(3 bits) B	B	B	B	+	+
	B	B	B	M	B_+	+	M
	-	B	B	B	B_+	+	M
	-	B	B	B	B_+ to +	+	M
	B	M	B	B	B_+ to +	+	M
	M	M	?	B	+	+	M
	M	M	?	+ ?	+	+	M
	th., tibia has definite op.						
	small, arboreal, toes not clawed but prehensile. Appearance and habits like phalangers.						
		fragmentary	ligamentous Sp.				
	$\frac{5,1,3,2}{4\ 1\ 3\ 3}$ lower M_4 er	$\frac{5,1,3,4}{3\ 1\ 3\ 4}$ worn	$\frac{5,1,3,4}{4\ 1\ 2\ 4}$ lower P_1 missing	$\frac{5,1,3,4}{4\ 1\ 3\ 4}$	$\frac{5,1,3,4}{4\ 1\ 3\ 4}$	$\frac{5,1,3,4}{4\ 1\ 3\ 4}$	$\frac{5,1,3,4}{4\ 1\ 3\ 4}$

Genus Myrmecobius.

Squirrel-like. Arboreal and terrestrial. Hallux absent. M. fasciatus, WRU, B546, ep. fusion same as in Antechinomys laniger, except lower limb eps. which were missing.

Family DIDELPHYIDAE:

Opossums. Arboreal. Pentadactyle, hallux opposable for climbing.

Genus Didelphys L.

Size of cat to a large mouse. Hind toes free.

8 skeletons were studied. D. virginianus, f, FM, 42697, was an adult. D. virginianus, EUZ, HH, 41.4 was rejected as it was not well macerated. Others are shown in (Table No. 82).

D. virginianus, f, FM, 47601 showed fusion of ep. 5, (16,17,31 & 32 missing)

" m, FM, (Dr. Davis's) -- humerus and phalanges missing

" WRU, B177 further fusion of ep. 3,6,7, 8,17?, 32?

D. cinerea WRU, B1349 further fusion of ep. 19,20

D. virginianus, m, FM, 41088 further fusion of ep. 16, 15 (some), 14 (some), 31, 30 (some), 29 (some)

Sub-Genus Philander:

P. laniger derbianus, f, FM, 50729 showed fusion of eps. 3,5 to 9,11,13 to 17,19,20,24,26 to 30

Philander sp., FM, 24142 showed further fusion of eps. 19,10,12,21,22,23, 25. (4 is 'R')

Last to fuse would be ep. 4

DISCUSSION.

From the sequences given above an approximate order can be computed as below:-

5,17,32	i.e.	Dist. elem. hum; term. phalanges
3,6(much retarded in Sarcophilus)	i.e.	Prox. elem. & dist. ep. hum.
16,31(retarded in Didelphys)	"	Middle phalanges
7,8(accelerated in Didelphys)	"	Epicondyles, humerus
15(19 & 20 in Didelphys)	"	Proximal phalanx, manus
30	"	Proximal phalanx, pes
13,14(accelerated in Sarcophilus)	"	Metacarpals
27,28,29	"	Metatarsals; calcaneal epiphysis
9,11	"	Proximal radius and ulna
18,19,20(much retarded in Sarcophilus)	"	Head and trochs. femur
24,26	"	Distal tibia & fibula
21,22,23	"	Distal femur; proximal tibia
25,10	"	Proximal fibula; distal radius
12	"	Distal ulna
4	"	Proximal humerus

The variations in the families are slight. Genus Didelphys L. of family Didelphyidae, seems to be a variant, since the humeral epicondyles, all phalanges, metacarpals and metatarsals, particularly epiphyses of the pes, are very slow to unite. But in Philander, a sub-genus of Didelphys, the evidence supplied by the two specimens studied supports the construction of the schedule given above. Sarcophilus, however, is a stronger variant, since it shows (i) retardation of fusion of distal ep. humerus (ep. 6) to a date after closure of all epiphyses of manus, (ii) a corresponding acceleration in the fusion of metacarpals when most of the phalanges of pes and all the distal epiphyses of humerus (except ep. 5) are still active, and (iii) considerable retardation in proximal femur, which is seen to close after fusion of proximal tibia and fibula, and distal radius and ulna, i.e., well ahead in the adolescent stage (p. 167) of Ungulates.

The above schedule shows that in this sub-order the line for closure of 'juvenility' may be drawn when proximal radius and ulna complete fusion, and that for 'puberty' after fusion of proximal femur, distal tibia and distal fibula. Adolescence would, therefore, include distal femur, radius and ulna and proximal tibia, fibula and humerus.

Further, the sequence presented above is remarkably similar to that found in the generalised mammals, Centetidae and Lemuroidea. Compared to Polyprotodontia, Diprotodontia represents not only a variety of morphological forms, shapes and sizes, reduction of teeth and toes, and syndactilism but a much more complicated and diverging pattern of epiphysunion sequence. Hence it appears that in having the more primitive number of teeth and less variations in form, shape, and size of its members and in the picture of the digits, and also from its manner of epiphysial fusion, Polyprotodontia is the more primitive form of Marsupials and a closer approach to the ancestral type than the Diprotodontia.

Epiphysial peculiarity in Polyprotodontia.

1. Terminal phalanges were epiphysial.

2. In Peragale lagotis, medial epicondyle fused both with shaft and distal epiphysis (trochlea) of humerus.

3. Sarcophilus ursinus, WRU, B238, was probably a menageric animal showing tartar in upper molars. This may be the cause of its showing a tardy union of epiphysis as compared to that seen in other specimens.

An epiphysial chart for Polyprotodontia is shown in Fig. 51. The Group-pattern of E.U.S. is shown in Fig. 52.

Table No.83
Order: MONOTREMATA

Fam.		E	c	h	i	d	n	i	d a e	Ornithorhynchidae
Genus									
Name		Tachyglossus aculeata	Echidna aculeata	Tachyglossus sp.	E.aculeata	Echidna	Echidna	Echidna	O.anatinus
Museum		F.M	I.M	A.M.N.H	E.U.Z	A.M.N.H	A.M.N.H	A.M.N.H	R.S
Number		42738	Sm.m.g	22839	HH 25	17355	42257	254	1889,123.6
Sex		Female	Male						
Age		Juv.	Juv.						Adult
A.EPIPHYSES									
1.Clav,	St.....								
2.	Ac.....								
3.Hum,	Pr.El..	Separate	Separate	G.T,Sep.	L.T,Sep.	M	M	M	Sep.
4.	" & Sh.	-	B	B	B	M	M	M	R
5.	Di.El..	Sep.	+	Sep.	+	M	M	M	+
6.	" & Sh.	-	B	B	+	M	M	M	+
7.	Lat.Ep.	B	B	B	B	M	M	M	+
8.	Med.Ep.	-	B	B	B	M	M	M	+
9.Rad,	Prox...	B	+	+	R	+	M	+	+
10.	Dist...	-	B	B	-	-	M	B	+
11.Ulna,	Prox...	B	B	B	B	B	M	+	+
12.	Dist...	-	B	B	-	-	M	B	+
13.Mc,	First..	+	+	+	+ or nil	M	M	M	+
14.	Rest...	+	+	+ or nil	+ or nil	M	M	M	+
15.Ph(M),	Prox...	+	+	+ or nil	+ or nil	M	M	M	+
16.	Mid....	+	+	+ or nil	+ or nil	M	M	M	+
17.	Term...	M	+	+ or nil	+ or nil	M	M	M	+
18.Fem,	Head...	-	-	B	B	M	B	M	+
19.	Gr.Tr..	-	-	B	B	M	B	M	+
20.	Ls.Tr..	B	B	B	-	M	B	M	+
21.	Dist...	-	B	B	-	M	B	M	+
22.Tib,	Con....	-	B	B	B	+	- to +	+	+
23.	Tb.....	-	B	B	B	+	- to +	+	+
24.	Dist...	-	B	B	B	-	B	B	+
25.Fib,	Prox...	-	-	-	B	B	B	M	+
26.	Dist...	-	B	B	B	-	B	M	+
27.Calc.	Epip...	+	+	+ or nil	+	M	M	M	+
28.Mt,	First..	+	+	+ or nil	+ or nil	M	M	M	+
29.	Rest...	+	+	+ or nil	+ or nil	M	M	M	+
30.Ph(P),	Prox...	+	+	+ or nil	+	M	M	M	+
31.	Mid....	M	+	+ or nil	+	M	M	M	+
32.	Term...	M	+	+ or nil	+	M	M	M	+
33.Ext.Centre...		All have Fabella							

B.SPL.FEATURE.. Powerful claws, toothless; ulna forms 2/3rd of total art. surface for wrist.

C.HABITS ETC... Ant-eater; terrestrial, some partly aquatic; burrowers (pes & manus webbed, webbing is no bar to burrowing).

D.REMARKS...... Captive Fixed by glue

The Order is a strange admixture of beast, bird & reptile. Proximal & Distal ep. of Humerus are mere flakes. The elements making up these epiphyses usually remain separate & distinct.

E.DENTITION.... Edentulous

THE STUDY OF EPIPHYSIS IN MONOTREMATA.

The Order Monotremata represents a link between Reptiles and Mammals in being oviparous and in having a reptilian type of pectoral gridle, non-epiphysial vertebrae, and other bony formations that are absent in other Orders of Mammalia. They have short pentadactyle limbs for burrowing or swimming or for both.

Family ECHIDNIDAE:

Burrowers. 5 clawed digits in each limb.

12 skeletons available for study. Of these 5 were adults, viz., Tachyglossus aculeata, f (EUZ, BC, VI,2; R.4020-1), Echidna aculeata (WRU, B175, and B547,m) and E. hystrix (RS, C11 and EUA, 23 XX,f).

Of the 7 young specimens, 3 from the American Museum of Natural History were fragmentary (Table No.83).

NOTE: The elements of proximal epiphysis of humerus were all separate in every case.

In T. aculeata, f (FM, 42738), there was fusion of eps. 13 to 17, 27 to 32

NOTE: A fabella was seen.

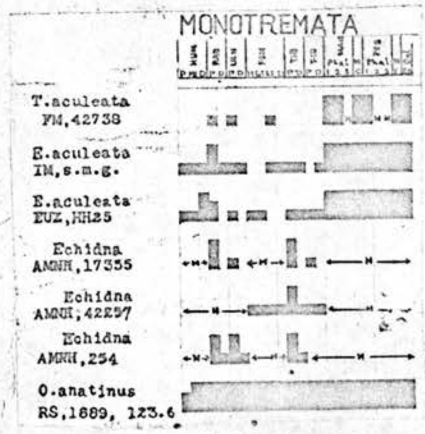
In E. aculeata, m (IM, s.n.g) further fusion of eps. 5,9

In Tachyglossus (AMNH, 22839) fusion was the same as above but existence of all ep. of manus was doubtful.

In E. aculeata (EUZ, HH,25) further fusion of ep. 6,(eps. in terminal phalanges and metapodia doubtful)

In Echidna (fragmentary, AMNH, 17355) further fusion of eps. 9,22,23,(hum. & fem. 'M') No ep. seen in phalanges

Fig. 54.



Epiphysial chart for Monotremata.

Abbreviations as in other charts.

In Echidna (fragmentary, AMNH, 42257) [illegible] humerus, radius & ulna 'M'. No ep. seen in phalanges.

" " " 254 humerus, femur, fibula, pes and manus 'M'. Fusion seen in ep.22,23

Hence, the fusion sequence as far as can be gathered is:-

All phalanges, metacarpals and metatarsals
Elements of distal ep. hum.; prox. radius
Distal epiphysis humerus

Proximal tibia

NOTE: ---- indicates absence of observation.

Family ORNITHORHYNCHIDAE:

Aquatic and burrowers. Pentadactyle webbed feet.

3 skeletons studied. All adults; O.anatinus, EUZ, HH .15; O. paradoxus, m, EUZ,BC,VI,2; and O. paradoxus,f, EUA, 23 XX.

DISCUSSION:

From the very meagre materials available for study no conclusion can be arrived at except that not only the termin but all other phalanges and even metacarpals and metatarsals may not have epiphysial ossification. In case they do have such epiphyses, their activity is closed earliest in the scale of fusion before any other epiphysis has had time to pull up with them. A chart of epiphysial fusion is annexed (Fig. 54).

Epiphysial peculiarity in Monotremata.

1. Proximal epiphysis humerus has three distinct elements, all separate.

2 1 2 3 3 1 3 3

2. Proximal fibula bifurcates and has an epiphysis on each fork, one articulating with femur, the other is free, (fabella ?).

3. Capitellum and trochlea may remain separate.

4. Terminal phalanges were often, and other phalanges, metacarpals and metatarsals more rarely, non-epiphysial.

2 1 2 3 3 1 3 3

Table No.84

Order:CHIROPTERA Sub-order:

S.Fam or Genus	Pteropidae	Vespertilionidae	
	Pteropus	Eptesicus	Myotis
Name	P.poliocephalus	E.serotina	Myotis sp.
Museum	E.U.Z	R.S	A.M.N.H
Number	MM77	1936,39.5	H.L.H's54
Sex			
Age	young		adult
A.EPIPHYSES			
1.Clav, St....	?	-	+
2. Ac....	?	B	+
3.Hum, Pr.El.	+	+	+
4. " & Sh.	B	-	+
5. Di.El.	+	+	+
6. " & Sh.	+	+	+
7. Lat.Ep.	+	+	+
8. Med.Ep.	*	+	+
9.Rad, Prox..	+	+	+
10. Dist..	B	-	B?
11.Ulna, Prox..	+	-	+
12. Dist..	nil	nil	nil
13.Mc, First.	B	?	+
14. Rest..	B	B	+
15.Ph(M),Prox..	B	B	+
16. Mid...	B	B	+
17. Term..	+ to nil	+ to nil	+ to nil
18.Fem, Head..	B	B	+
19. Gr.Tr.	?	?	+
20. Ls.Tr.	?	?	+
21. Dist..	-	-	+
22.Tib, Con...	R to +	-	+
23. Tb....	+	?	+
24. Dist..	B	B	+
25.Fib, Prox..	nil	nil	nil
26. Dist..	B	*	+
27.Calc. Epip..	?	?	+
28.Mt, First.	+	?	+
29. Rest..	+	B	+
30.Ph(P),Prox..	+	B	+
31. Mid...	+	+	+
32. Term..	+	+	+
33.Ext.Centre..			
B.SPL.FEATURE.	*med.ep.is not an ep.proper but is a sesamoid	*ep.26 is calcified; olecranon patella-like & is joined to med. epic.by ligt.	
C.HABITS ETC..			
D.REMARKS.....	spec.in a sealed glass box; study ?	manus & pes, ligamentous	
E.DENTITION...	M_3 not in	$\frac{2,1,1,3}{2\ 1\ 2\ 3}$	$\frac{2,1,3,3}{3\ 1\ 3\ 3}$

THE STUDY OF EPIPHYSIS IN CHIROPTERA.

Flying mammals, fore-limbs modified for flight. Fingers extraordinarily elongated. Large medullary cavities in bones. Clavicle always present. Both limbs pentadactyle; anterior larger than posterior. Metacarpals and phalanges of digits 2 & 5 are greatly elongated. Digits 1, 4 & 5 of manus have 2 phalanges; in digits 2 & 3 the number varies. 3rd finger is the longest. Ulna small and ankylosed with radius. Hind limbs rotated outwards, knee directed backwards and sole of foot forwards; hallux external. Fibula usually reduced.

There are two Tribes:

Tribe 1. Megachiroptera or frugivorous bats

Tribe 2. Microchiroptera or insectivorous bats

M E G A C H I R O P T E R A:

2nd finger clawed. Tail short (Table No. 84).

Family PTEROPIDAE:

3 skeletons studied, 2 of which were adult with both clavicular epiphyses fused (Pteropus intermedius, MUA, L23, IX ; P. celaens, RS, 1932, 64.4).

In P. poliocephalus, MUZ, NN,77, there was fusion of eps. 3, 5,6,7,9,11,17,22,23,28 to 32

NOTE: Epiphysis for medial epicondyle remained as a separate ossicle or sesamoid bone attached by ligaments.

MICROCHIROPTERA:

2nd finger not clawed and has one phalanx.

(Table No.84).

Family VESPERTILIONIDAE:

Eptesicus (Vesperugo)

2 skeletons studied, 1 was an adult (V. noctila RS, 1932, 64.6).

In E. Serotina, RS,1936, 39.5, there was fusion of eps. 3,5 to 9, 17, 31, 32

NOTE: In this specimen olecranon was present as a sesamoid bone, like patella.

In Myotis sp, (AMNH, H.L.Hills' No.54) there was further fusion of 1,2,4,11 to 16, 18 to 27

Hence, last epiphysis to fuse would be ep. 10

16 more skeletons of different families of Microchiroptera were examined. All limb epiphyses, including both ends of clavicle, were fused in them.

Examination of the fusion in the 3 specimens, therefore, shows the following sequence:-

3,5,6,7,8,9,17, 31,32	i.e.	Terminal phalanges, all; mid. phal., pes; prox. & dist. elem., and all dist. eps. hum.; prox. radius
11,22,23,28,29,30	"	Prox. phal., pes ; metatars. prox. ulna and tibia
13,14;15,16;18,19, 20;21;24;26;27; 12;4;2,1	"	Calcaneal ep.; mid. & prox. phal., manus; metacarps., prox. & dist. fem.; dist. tib. & fib.; dist. ulna; prox. hum.; both epiphyses clavicle.
10	"	Distal radius

DISCUSSION:

As in most mammals, the terminal phalanges (eps. 17 & 32) are the first to fuse. An inspection of the anatomy of bats and the attachment of their patagium, and a review of the requisites for maintaining an animal in flight, reveal that in bats the wings have to be enlarged sufficiently widely to entangle a column of air that may offer sufficient resistance to buoy up the animal against gravity and give it the friction required in its flights. It is necessary, therefore, that the growth in length of those bones that are essential in making up the proper dimension of the wing be allowed to continue unhampered, and also those which form the fulcrum of the wing be consolidated early. This may be considered to be the reason why the epiphyses of pes (eps. 31, 30; 28 & 29) are the earliest to fuse along with those of bones at the elbow (eps. 5,6,7,8; 9 & 11), which are involved in the continuous flappings of the wings. Besides, the fusion in the bones of pes seemsto be relatively early, because they are not included in the patagium. Hence, not being under the influence of retardation, their fusion indicates apparent acceleration.

They are immediately followed by fusion of, i.e., consolidation at, the proximal tibia. Hence the first stage in the sequence of fusion of epiphyses in bats may be written as -

17,31,32	i.e.	Terminal phalanges, manus & pes; middle phalanx , pes
3,5,6,7,8,9	"	Prox. & dist. elements and all distal eps., humerus; proximal radius
11,30,28 & 29	"	Prox. ulna; prox. phal., pes; metatars.
22,23	"	Proximal tibia

If the hypothesis given above be correct then the step represented in the Myotis sp. (AMNH, H.L. Hill's No.54) may be simplified by breaking it up into a successive series of fusion as follows:-

(i) Since proximal tibia has fused in the stage represented by E. serotinus (RS,1936, 39.5), it indicates strain at knee and a collateral fusion in distal femur (ep. 21) is to be expected. Fusion of proximal humerus (ep. 4) is also to be presumed since the position of humerus in bats indicates that the bone is used as a pivot on which the whole wing turns as a flap. Growth in length of the pivot would not materially add to the length of the wing, hence the fusion of distal humerus will, without further delay, be followed by consolidation of the upper end of the pivot (proximal humerus or ep. 4) and the shoulder arch (lateral ep. clav. or ep. 2). Hence the fusion is -

Eps. 21,4,2 (dist. femur, prox. hum., lat. clavicle).

(ii) The next step is the fusion of -

Eps. 24,26,27; 18,19,20 (calc. ep.; dist. tibia & fibula; prox. fem. & trochs.).

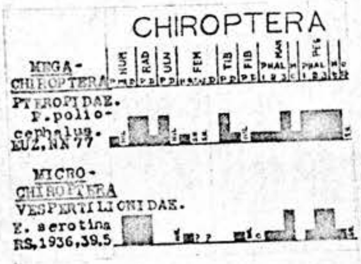


Fig. 55.

Epiphysial chart for Chiroptera.

Abbreviations same as in previous charts. Hatching indicates unequal epiphysial activity on opposite sides or in different members of the same side.

- - - -   - - - -   - - - -

Now is the turn for the two ends of the lower limb to be consolidated. The pressure of air fills up the wing in flapping and, like a sail, makes it convex dorsalwards and concave ventrally. Thisis helped by the knee being turned dorsalwards and the epiphyses round it (knee), already fused. The net result is that strain is borne at the ends, i.e., at the ankle and hip, just as in a stretched bow the pressure is greatest at the ends where the string is fixed.

(iii) The metacarpals and phalanges and sternal epiphysis of clavicle have been growing to their maximum and are now called on to fuse thus:-

Eps. 13,14,15,16,1(metacarps.; prox. & mid. phals., manus; sternal ep. clavicle)

(iv) The final epiphyses to fuse will be those at the wrist and the arrangement, as in the specimen of Myotis sp., suggests fusion of -

Ep. 12 (distal ulna) followed by
" 10 (distal radius).

Epiphysial peculiarity in Chiroptera.

1. Terminal phalanges, except those that bear claw, do not have any epiphysis. Similarly there may not be any ep. at the middle phalanx. These grow by non-epiphysial ossification from shaft, as explained in page 17.

2. Olecranon and medial epicondyle may remain as separate ossicles, like patella. This may explain the origin of 'traction epiphyses' (see pp.8 & 9).

3. Fibula has no proximal epiphysis and is not joined to tibia or femur by ligaments.

For epiphysial chart see Fig. 55.

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Table No. 85

Order: CARNIVORA Sub-order: Pinnipedia

S.Fam or Genus	Trichecidae		O t a r i i d a e			
	Trichechus		Otaria		Zalophus	
Name	T. rosmarus	T. rosmarus	O. californianus	Otaria	Z. californianus	Z. californianus
Museum Number	R.S. Top c.20&21	E.U.A. P.Tr.r.1	W.R.U. B 1054	W.R.U. F.E.R's	W.R.U. B 75	W.R.U. B 637
Sex						Female
Age	adult	adult		young		young (3 years)
A. EPIPHYSES						
1. Clav, St....	nil	nil	nil	nil	nil	nil
2. Ac....	nil	nil	nil	nil	nil	nil
3. Hum, Pr.El.	+	+	-	+	+	+
4. " & Sh.	+	+	-	R	+	+
5. Di.El.	+	+	-	+	+	+
6. " & Sh.	+	+	-	+	+	+
7. Lat.Ep.	+	+	-	+	+	+
8. Med.Ep.	+	+	-	+	+	+
9. Rad, Prox..	R	+	-	B	+	+
10. Dist..	-	-(L.U)	-	B	- to B	R
11. Ulna, Prox..	R	+	-	A*	+	+
12. Dist..	-	R	-	B	- to B	+
13. Mc, First.	-	B	B_	M	R	+
14. Rest..	-	B	-	M	R to +	+*
15. Ph(M), Prox..	-	- to B	-	M	M	M
16. Mid...	-	B	B	M	M	M
17. Term..	+	+	+	M	M	M
18. Fem, Head..	R	+	-	B	B	R
19. Gr.Tr.	+	+	-	B	-	R
20. Ls.Tr.	+(Gl)	+	-	B	-	+
21. Dist..	+	+	-	B	B	B_+
22. Tib, Con...	+	+	-	B	B	R
23. Tb....	+	+	-	nil	B	+
24. Dist..	-	R	-	B	B	R
25. Fib, Prox..	+	+	-	B	M	R
26. Dist..	B	R	-	B	M	R
27. Calc. Epip..	+	+	B	B	+	R
28. Mt, First.	-	R	-	B	R	B_+
29. Rest..	-	R	B_	B	R to +	B
30. Ph(P), Prox..	-	R	B	B	M	B
31. Mid...	- to B	R	B	B	M	+
32. Term..	+	+	+	B	M	+
33. Ext. Centre..				talus has an ep. at caudal end		*ep. at head & base of outer 4 metacarpals
B. SPL. FEATURE.	styloid ulna artic. with prox. carpals					
C. HABITS ETC..	aquatic, but use hind limbs on land		aquatic, hind limbs turned forwards beneath body and can support it in locomotion			
D. REMARKS.....	animals very bulky, phalanges in various grades of union in the same row			*ep. line not clearly seen, not fully ossified	fragmentary	zoo specimen
E. DENTITION...	1.1.3 / 0 1 3	1.1.3 / 0 1 3	3.1.4.1 / 2 1 4 1	3.1.4.1 / 2 1 4 1	3.1.4.1 / 2 1 4 1	M

Table No. 86

Order: CARNIVORA Sub-order: Pinnipedia

	Otariidae			Phocidae				
...s.				Phocinae				Cystophorinae
...s	Otaria	Eumetopias	Zalophus	Phoca			Halichoerus	Cystophora
...	O.joubata	E.sinerea	Z.californianus	P.vitulina	P.vitulina	P.vitulina	H.grypus	C.cristata
...um ...er	R.S. C 24	E.U.A. E.p.Eu.cin.2 Male adult	W.R.U. B 315	E.U.A. 52LIV baby	I.M. m.g.36 v.young	R.S. C 24	E.U.A. 33XVI Male y.adult	R.S. gal.
	nil	nil	nil	nil	nil	nil	nil	nil
	nil	nil	nil	nil	nil	nil	nil	nil
	+	+	M	ct.	+	+	+	+
	R	+	M	-	B	- to B	R	+
	+	+	M	B	+	+	+	+
	+	+	M	-	-	+	+	+
	+	+	M	ct.	-	+	+	+
	+	+	M	ct.	-	+	+	+
	+	B	M	-	B	+	+	+
	+	B to R	M	-	-	-	B	+
	+	R	M	-	-	B	R	+
	R	B to R	M	-	-	-	B	+
	R	B to +	M	-	-	-	R	+
	+	B to +	M	-	-	-	R	+
	R to +	B to R	M	-	-	-	R	+
	+	E to R	M	-	-	B	+	+
	+	+	M	-	+	+	+	+
	+	+	+	-	-	+ or nil	R	+
	+	+	+	-	-	R	R	+
	+	+	+	nil	nil	nil	nil	nil
	R	+	+	-	-	- to R	B	+
	R	+	+	-	-	- to B	R	+
	R	+	+	nil	nil	- to B	nil	+
	B_+	B to +	B_+ to +	-	-	- to B	-	R
	+	+	+	-	-	-	B	+
	B	B to +	B_+ to +	-	-	- to B	-	R
	+	+	M	-	-	+	+	+
	+	-	M	-	-	-	-	+
	+	-	M	-	-	-	B	+
	+	B to R	M	-	-	-	B	+
	+	B to R	M	-	-	-	R	+
	+	+	M	-	- to B	+	+	+
	delt. crest v. pro. no op.	delt. crest v. prom. no op.			op. B art. with cl. & sh. hum.			

hind limbs stretched backwards, can not be used in locomotion on land. fore limbs can support body.

Mc_1 strongest, Mc_5 shortest but widest, optic. fem. has
non-op. cartilaginous ossification in Skel. no proper
deltoid crest hd.

stand.	Stand.	M	stand.	stand.	stand.	stand.	stand.

THE STUDY OF EPIPHYSIS IN PINNIPEDIA.

Aquatic Carnivora. Form fish-like but not so completely as the whales and sirenia. Short pentadactyle fin-like limbs, digits united by membrane. Nails short or absent, occasionally well developed. Clavicles absent. Ulna and radius separate. Number of phalanges may be more than normal.

Family OTARIIDAE:

Eared seals. Hind limbs with toes turned forwards beneath the body and capable of supporting it in locomotion on land.

7 skeletons studied.(Tables Nos. 85 & 86).

Genus Otaria or Zalophus.

In skel. O. californianus, WRU, B1054 fusion of ep. 17,32

" " " " " (Mr. Randall's collection) further " " " 3,5,6,7, 8 (phal. pes 'B' & manus missing)

" " " " " B75 further fusion of ep. 4,9,11, some 14 & 29 (manus & pes 'M'

" " " " " B637 " " " " 12,13,14,20,23,31 (phals. manus,'M'; 28 & 29 'B')

" " " jöubata RS,C24 further fusion of ep. 16,18,19, 25,27 to 30

" " " californianus WRU, B315 further fusion of ep. 21,22,24,26 (24 & 26 'B' on right side)

NOTE: In Mr. Randall's specimen talus has an epiphysis posteriorly.

In specimen WRU, B637, an epiphysis was seen at head and base of each of outer four metacarpals. Ep. at head Mc5 was 'B'.

Genus Eumetopias.

In skel. E. cinerea, m, EUA, 1.P.Eu.cin.2 fusion of ep. 3 to 8,13 & 14 (left), 17 to 23, 24 (right), 25,32

Family TRICHECHIDAE: (Table No.85).

Walruses. No external ears. Very bulky body. Position of limbs as in eared seals. Manus has sub-equal digits.

2 skeletons studied.

In skel. T. rosmarus, RS,C 20 & 21 fusion of ep. 3 to 8,17, 19 to 23,25,27,32(20 glazed; 15,26,31,'B' to '-'; 9,11, 18, 'R')

" " " " EUA,P.Tr.r.1 further fusion of ep. 9,11, 18 (12,24,26,28 to 31 are 'R' and may be considered as closed; 13,14,16 are 'B'; & 10,15 are '-')

NOTE: Phalangeal epiphyses were in various grades of union.

Family PHOCIDAE. (Table No.86).

Earless seals. Hind limbs directed backwards and cannot be used for locomotion on land. Fore limbs can support body. Outer digits of pes longer than middle.

5 skeletons studied.

Sub-Family Phocinae.

Genus Phoca L.

In skel. P. vitulina, EUA, 52, LIV	fusion of ep. nil
" " " " IM, C 36, m.g.,	" " " 3,5,17 (20 nil)
" " " " RS, C24, further	" " " 6,7,8,9, 18,27,32(19 is 'R', 20 nil)

Genus Halichoerus.

In skel. H. grypus, m, EUA, 52, XVI, there was fusion of ep. 3, 5,6,7,8,9,16,17,27,32 (20 & 23 nil): 4,11,13,14, 15,18,19,22,31 are 'R'

Sub-Family Cystophorinae.

Genus Cystophora.

In skel. C. cristata, RS, gal, there was fusion of ep. 3 to 19,21,22,23,25,27 to 32 (20 is nil, 24 & 26 'R')

Presumably, last to fuse would be ep. 24 & 26

DISCUSSION:

It is said that Pinnipedians are Carnivores that have taken to the water. They present three families; all of which are adapted to a marine existence in an increasing degree of perfection. The limb has been shortened and the greater part of it is covered by the common integument of the body. Nails tend to disappear and phalanges are occasionally increased in number. Digits are joined together by a web of skin which may be longer than the toes; a flipper is thus formed. In Otariidae and Trichechidae the posterior limbs have toes looking forwards; they support the body in locomotion. These animals still maintain their connexion with land. The otariidae retains the ear, showing that its aquatic adaptation is less perfect and more recent than the earless Trichechidae. By far the most advanced adaptation to a watery existence is seen in the earless seals, Phocidae. They have assumed a fish-like body; their posterior limbs are turned backwards and fixed to the tail by a common integument and they do not support the body on land, where the locomotion is effected by a wriggling movement of the body. The seals rarely come to land except for breeding.

Below is given the order of fusion as seen in the three families:-

Otariidae

Term. phals.
Elems. prox. hum.; all ep. dist.hum.
Prox.rad.& ulna;prox. hum.;some metacarps & metatars.
Metacarps.;mid.phal. pes; lesser troch. fem.; tub.tib., dist. ulna
Mid.phal.manus;prox. phal.pes;calc.ep.; all metatarsals; head & gr. troch. fem.; prox. fib.
Dist. fem.;prox.tib.; dist.tib. & fib. (in Eumetopia, dist.ulna & mid. & prox. phals. are still open)
Prox.phal.manus;dist.rad.

Trichechidae

Term.phals.;elem.prox.hum.; all ep. dist.hum.;prox.hum.; trochs.fem.;calc.ep.;dist. fem.;prox.tib.;prox.fib.(prox. rad.,ulna & fem. are 'R').
Prox.rad.,ulna & fem.

Dist.ulna,tib. & fib.; metatarsals; mid. & prox. phals., pes.
Metacarps., mid. phal. manus.

Prox. phal. manus; dist. radius.

Phocidae.

Term.phal. manus
Prox. & dist. elem. hum.
Term. phal. pes; dist. ep. & epiconds., hum.; prox. rad.; head and lesser troch. femur; calc. epiphysis
Mid. phal. manus

Prox. hum. & ulna; prox. phal. manus; mid. phal. pes; metacarps; greater troch. femur; proximal tibia.

Metatarsals; prox. phal. pes; dist. fem.; distal radius ; distal ulna.
Distal tibia ; distal fibula

On reviewing the above sequences, it is seen that the order of union is not the same in all the families. They agree in certain principles of fusion. First, in all of them is still evident the primitive character of union of epiphyses in land mammals viz: the early fusion of terminal phalanges and all epiphyses at distal humerus. But the picture changes in other epiphyses. The more advanced the aquatic adaptation, the more upset is the order of fusion as compared to land mammals. In all the families, proximal humerus fuses very soon after the terminal phalanges and distal epiphyses of humerus are consolidated, probably in response to the strain thrown at the shoulder in backward strokes originating therefrom while swimming. Secondly, the fusion in distal tibia and fibula is delayed owing to removal of the need for consolidating the ankle in aquatic animals in which swimming is effected by propulsive force originating at the knee. Hence distal femur and proximal tibia and fibula

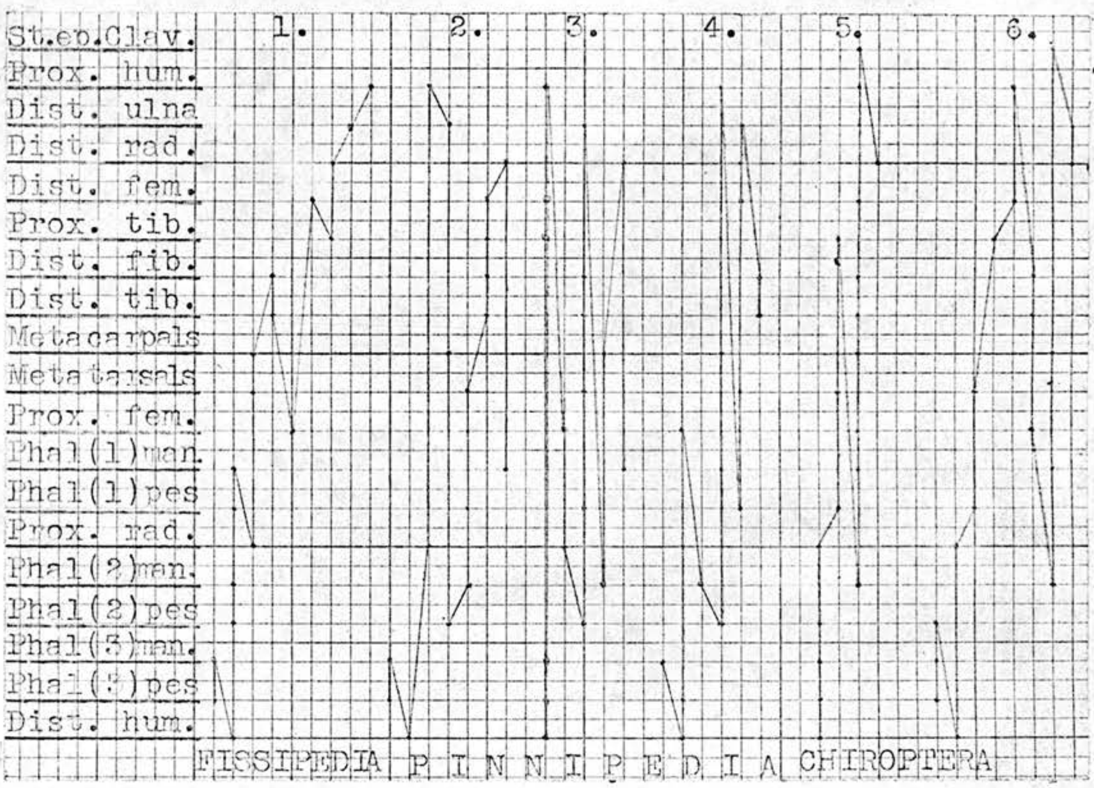


Fig. 56.

Graphs showing the Sequence of Epiphysial Fusion in Fissipedia compared to that in the Aquatic adaptations of Pinnipedia. The complete Volant adaptation of Chiroptera is also shown for comparison. Acceleration of fusion of proximal humerus is noticeable in both the adaptations, specially in the Aquatic.

1. Fissipedia (Felidae). 2. Otariidae. 3.Trichechidae

4. Phocidae. 5. Chiroptera as actually observed(p.217).

6. Chiroptera - observations spread out (pp.219-220).

will fuse earlier than distal tibia and fibula. As a matter of fact, in the most perfectly adapted animal of the group, the Phocidae, these two are the last of all long bone epiphyses to fuse. Thirdly, fusion in phalanges other than the terminal is very slow and may be put off till almost the last date.

Union of the remaining epiphyses is different in the three families and corresponds usually to the quality of adaptation that any of them has attained. For instance, in the least adapted, viz: the eared seals, the relative position of fusion in proximal radius, ulna and femur, metacarpals, metatarsals, distal femur, proximal tibia and fibula and distal radius and ulna is more or less as in land mammals; but with more advanced adaptation in Trichechidae, epiphyses at the knee (distal femur, proximal tibia and fibula) have been accelerated and fuse earlier than proximal radius and ulna. With still better aquatic adaptation, as in Phocidae, everything else has been accelerated over distal tibia and fibula, and the ankle has joined and even excelled the normal tardiness of fusion of epiphyses at the wrist as in most land mammals.

For epiphysial chart and group pattern of E.U.S. see Figs. 32 & 34. For comparative graphs see Fig. 56.

Table No.87

Order: SIRENIA Sub-order:

Fam.					
Genus	M a n a t u s (T r i c h e c u s)				
Name	T.inunguis	T.manatus	T.senegalensis	T.manatus	T.manatus
Museum	A.M.N.H.	A.M.N.H.	A.M.N.H.	A.M.N.H.	A.M.N.H.
Number	94164	nil	53939	24295	91096
Sex			female		
Age					
A.					
1.					
2.					
3.	-	M	separate	separate	separate
4.	-	-	-	+	+
5.	?	?	+	+	+
6.	-	-	B	+	+
7.	-	-	-	+	+
8.	-	-	-	+	+
9.	-	-	?	+	+
10.	ct.	-	-	+	+
11.	-	ct.	ct.	+	+
12.	ct.	B(L.U)	ct.	+(patches of L.U)	+
13.	-	- to +	-	+(partly L.U)	+
14.	-	- to +	-	do.	+
15.	-	- to B	- to B	+	+
16.	-	B	- to B	+	+
17.	-	B	- to B	+	+
18.					
19.					
20.					
21.					
22.					
23.					
24.					
25.					
26.					
27.					
28.					
29.					
30.					
31.					
32.					
33.					

All metacarpals have epiphyses at distal ends, proximal ends being covered by cartilage and porous, suggesting growth activity. Phalanges 1 & 2 have ep. at both ends, the 3rd having ep. at proximal end only.

prox. rad. ct.
covered like
prox. metacarpals

All have two incisors visible in jaw but unerupted, several teeth are well worn, some lost, some unworn. All molariform. Grinding teeth, 7 to 11 pairs, succeed from behind forwards as in elephants.

THE STUDY OF EPIPHYSIS IN SIRENIA.

Aquatic. Hind limb and clavicle absent. Fore-limb paddle-shaped and very moveable at all its joints. Bones of arm and hand articulate together as in land mammals. Digits five. Number of phalanges the same as in land mammals or show "at most traces of increase above the normal" (Beddard[70]). Bones are heavy and without medullary cavity.

Manatus - Vestiges of 2 or 3 nails in manus.

5 specimens (Table No.87) studied, by kind permission of Prof. W. K. Gregory and Dr. H. E. Anthony, at the American Museum of Natural History, New York.

In skel.	94164,	there was	fusion of ep. nil
" "	no number	" " further	" " " metacarpals (some)
" "	53939, f	" " "	" " " dist. elem. hum. (metacarps. '-'; prox. rad. cartilage covered)
" "	24295	" " "	" of ep. prox. hum., epicond. & dist. ep. hum.; prox. & dist. rad.; prox. & dist. ulns; metacarps. & phals. (patches of lapsed union in distal ulna & metacarps.)
" "	91096	" "	" of all ep. and no lapsed union

some teeth lost   incisors only seen

Table No. 88

Order: SIRENIA Sub-order:

S.Fam or Genus	H A L I C O R E				
Name	H.dugong	H.dugong	H.dugong	H.dugong	H.dugong
Museum Number	E.U.A. L 23 XLI	I.M. Mam. gal.	R.S. Top C25&26	E.U.A. L23 XL A&B	E.U.A. S.Hal d 1
Sex,					Male
Age	immature	immature	young		
A.EPIPHYSES					
1.Clav, St....					
2. Ac....					
3.Hum, Pr.El.	-	-	Hd.& G.T.sep.	Hd.& G.T.sep.	+
4. " & Sh.	-	-	-	-	+
5. Di.El.	+	+	+	+	+
6. " & Sh.	-	-	-	+	+
7. Lat.Ep.	-	-	+ or nil	+	+
8. Med.Ep.	-	-	+	+	+
9.Rad, Prox..	-	nil	+	+	+
10. Dist..	-	-	-	-	R
11.Ulna, Prox..	-	B	B	R	+
12. Dist..	-	-	-	-	R
13.Mc, First.	-	-	nil ?	nil ?	nil ?
14. Rest..	-	-	-	B ?	+
15.Ph(M), Prox..	-	-	- to B	-	+
16. Mid...	-	-	B	-	+
17. Term..	M	-	nil ?	-	+
18.Fem, Head..					
19. Gr.Tr.					
20. Ls.Tr.					
21. Dist..					
22.Tib, Con...					
23. Tb....					
24. Dist..					
25.Fib, Prox..					
26. Dist..					
27.Calc. Epip..					
28.Mt, First.					
29. Rest..					
30.Ph(P), Prox..					
31. Mid...					
32. Term..					
33.Ext.Centre..					
B.SPL.FEATURE.	Metacarpals have ep. at both ends; same with ph.1&2	Mc.& ph. have ep. at both ends	ph.1&2 have ep. at both ends	ph.1&2 have ep. at both ends	Mc. have ep. at both ends
C.HABITS ETC	Totally aquatic				
D.REMARKS.....	Distal ulna & radius are equally important in supplying articulation to carpals. Phalanges are unequal in number.				
E.DENTITION...	1,0,0,2 / 1 0 0 3 some tooth lost	1,0,0,0 / 1 0 0 0 incisors only seen	1,0,0,3 / 0 0 0 2	M	2,0,0,2 / 1 0 0 3

NOTE: The centres of ossification for proximal humerus were separate. All metacarpals had epiphysis at distal ends; their proximal ends were covered with cartilage and were porous, suggesting growth activity. Phalanges 1 and 2 had epiphysis at both ends. Phal. 3 had epiphysis at proximal end only.

Halicore - Manus has no nails.

5 skeletons studied (Table No.88). The following was noticed:-

In skel.	EUA, L23 XLI) & IM, m.g.)	fusion of ep.	dist. elem. hum.
" "	RS, C25 & 26 further	" " "	lat. & mid. epics. hum. (doubtful whether they were ep. ossifications) proximal radius
" "	EUA, L23XL a&b	" " " "	dist. ep.hum., prox. ulna
" "	EUA, S.Hal.d.l,m	" " " "	prox. elem. and ep. hum.; metacarps. & phals.

Presumably the last to fuse would be ep. distal radius and distal ulna

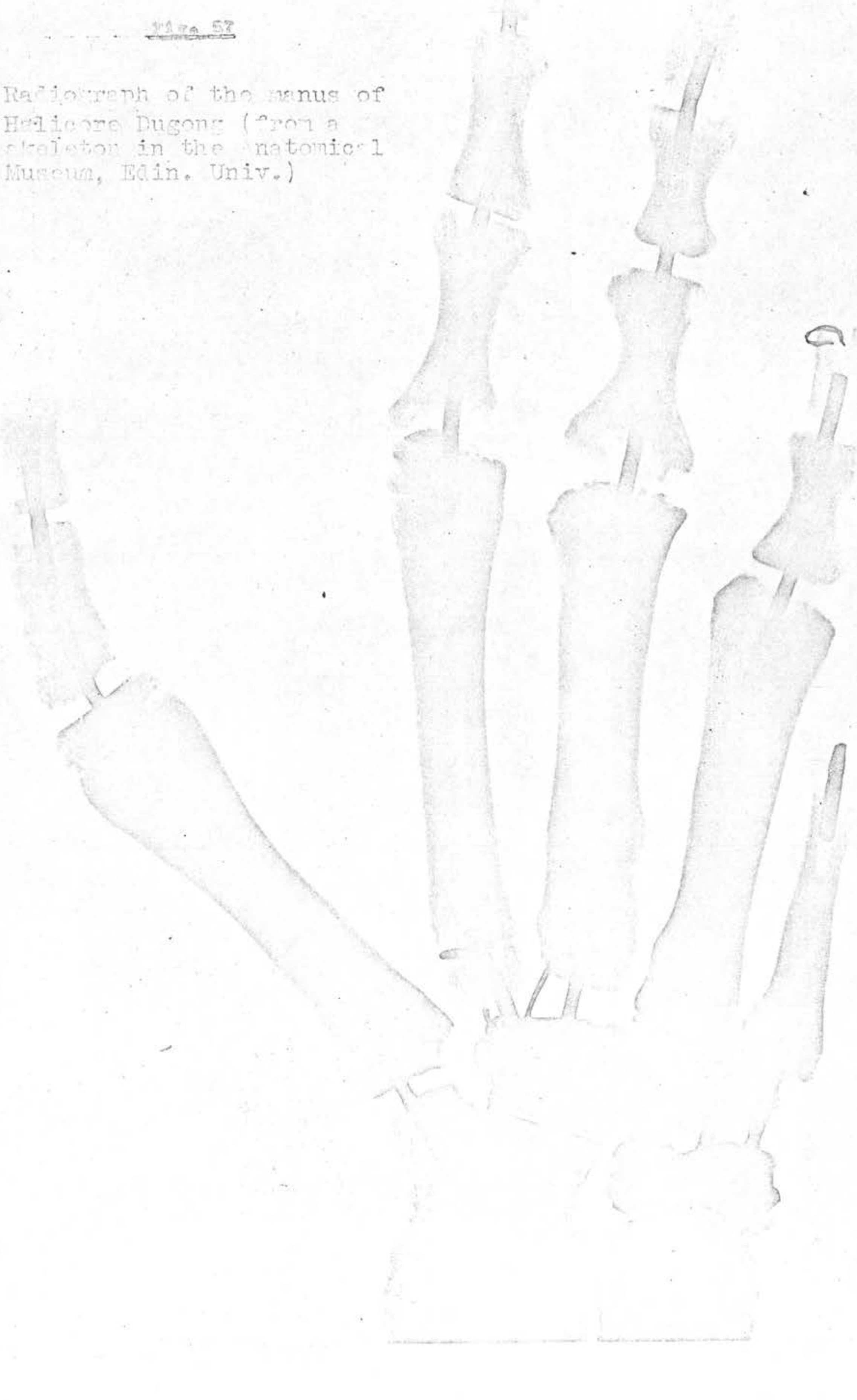
NOTE: In specimens RS, C25 & 26 and EUA, L23XL a & b, head and greater tubercle of humerus were separate. Metacarpals and phalanges, except the terminal, had epiphysis at both ends. Phalanges were unequal in number. Epiphysis for first metacarpal was doubtful in 3 out of 5 specimens.

Attempting to graft the sequence of fusion in the two species, the following is obtained:-

Some metacarpals
Distal elements of humerus
Epicondyles humerus; proximal radius
Distal epiphysis humerus; proximal ulna
Proximal humerus; metacarpals; phalanges
Distal radius and distal ulna

Fig. 57

Radiograph of the manus of Halicore Dugong (from a skeleton in the Anatomical Museum, Edin. Univ.)



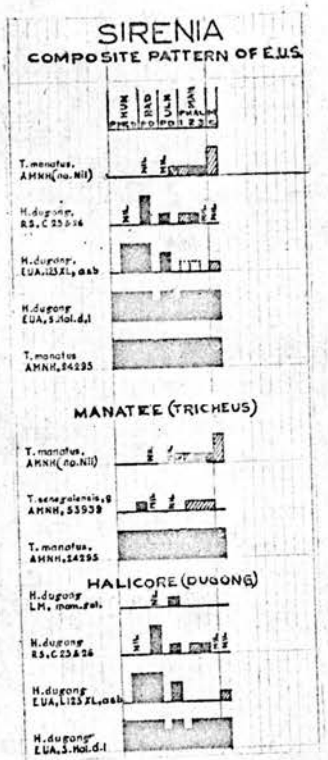


Fig. 58

Epiphysial chart for Sirenia.

Fig. 69

Epiphysial chart for Cetacea.

Abbreviations are the same as in other Epiphysial charts. Hatching indicates a difference in the stage of epiphysial activity on the two sides or amongst similar members on the same side. A clear circular space with an asterisk or the letter G within indicates 'glazing' of the epiphysis.

DISCUSSION:

Here again as in the case of ungulates the fusion of metacarpals extends long and covers almost the whole range of epiphysunion period, specially in Manatee. Proximal radius and epicondyles and distal epiphysis of humerus keep their position as in ungulates. The special features are, (a) the very late fusion of phalanges, (b) the distal ulna and radius are the last epiphyses to fuse and (c) proximal humerus fuses earlier than in land mammals.

The possession of epiphyses at both ends of metacarpals and phalanges 1 and 2 is an aquatic adaptation. The fusion in metacarpals shows that strain is earliest brought to bear on them but, as with all other epiphyses in aquatic animals, the urge to unite is soon lost and the epiphyses proceed liesurely towards fusion, some never uniting at all (lapsed union, see Fig. 57). This loss of urge is due to buoyancy in an aquatic medium and consequent loss of pressure on articular surfaces.

From a consideration of the union of trunk epiphyses and its correlation with tooth eruption and fusion of limb epiphyses Todd & Todd[81] have confirmed the biologists' conception of the affinity of Sirenia to Ungulata. The present study has no presumptions in the matter.

In Fig. 58 is given a composite pattern of E.U.S. for Sirenia.

Epiphysial Peculiarity in Sirenia.

These have already been mentioned. The metacarpals and proximal and middle phalanges have epiphysis at both ends, one or both of which may not develop an ossific centre. Similarly, it is doubtful whether an ossific epiphysis at all appears for the epicondyles of humerus.

THE STUDY OF EPIPHYSIS IN CETACEA.

Perfectly aquatic, fish-like, without hind limbs. Anterior limbs represented by short externally unjointed flippers which can only be moved as a whole. Digits entire and enclosed in a common integument; phalanges usually exceed the normal number in mammals. Posterior limbs represented by skeletal rudiments.

Clavicles absent. Humerus short and freely moveable upon scapula. Other joints of fore-limb imperfect. Radius and ulna flattened and short. In whalebone whales many of the elements of manus including phalanges remain cartilaginous. Usually 5 digits. More than 3 phalanges in some digits. Phalanges have epiphyses at both ends. Fore-limbs do not apparently serve as organs of locomotion so much as balancers and in clasping the baby to the breast.

It is divided into two Sub-Orders:-

1. Mystacoceti or Whalebone or True whales.
2. Odontoceti or Toothed whales.

Table No. 89

Order: CETACEA Sub-order: Mystacoceti

Fam. or Genus	Balaenidae		Balaenopteridae					
	Balaena	~~Balaen-optera~~	B a l a e n o p t e r a					
Name	B.mysti-cetus	B.mysti-cetus	B.ros-trata	B.ros-trata	B.bore-alis	B.sib-baldi	B.sib-baldi	B.musculus
Museum	E.U.A.	E.U.A.	E.U.A.	E.U.A.	E.U.A.	E.U.A.	E.U.A.	E.U.A.
Number	C.B.M.1	C.B.M.24	C.Bpt.R1	C.Bpt.R2	C.Bpt.B1	Bpt.S 23	Bpt.S22	C.Bpt.M 9
Sex		Male		Fem.		Fem.	Male	Male
Age	young	young		adult		young	adult	adult
A.EPIPHYSES								
1.Clav, St....								
2. Ac....								
3.Hum, Pr.El.	+	+	+	+	+	+	+	+
4. " & Sh.	B-(L.U)	B	B	+	B?	B	+	+
5. Di.El.	+	+	+	+	+	A	+	+
6. " & Sh.	B-(L.U)	B	B	B	B?	+	+	+
7. Lat.Ep.								
8. Med.Ep.								
9.Rad, Prox..	B-	B-	*-	+	B-	B	+	+
10. Dist..	-	B-	nil	B(in bits)	*-	nil	B- ?	B
11.Ulna, Prox..	B- ?	B-	**B-	+	B	B	+	+
12. Dist..	-	B-	nil	B(bits)	*-	nil	B- ?	B
13.Mc, First.								
14. Rest..								
15.Ph(M),Prox..								
16. Mid...								
17. Term..								
18.Fem, Head..								
19. Gr.Tr.								
20. Ls.Tr.								
21. Dist..								
22.Tib, Con...								
23. Tb....								
24. Dist..								
25.Fib, Prox..								
26. Dist..								
27.Calc. Epip..								
28.Mt, First.								
29. Rest..								
30.Ph(P),Prox..								
31. Mid...								
32. Term..								
33.Ext.Centre..								
B.SPL.FEATURE.								
C.HABITS ETC..								
D.REMARKS.....		manus set in plaster	*ep. repr. by a st. covering only **ep.cov. partly os-sified.		*in bits		both ends of [illegible] are tipped with cart, no bony ep.	
E.DENTITION...								

Table No. 90

Order: CETACEA Sub-Order: Odontoceti

am.	P h y s e t e r i d a e				Platanistidae	D e l p h i n i d a e			
enus	Hyperoodon	Mesoplodon			Platanista	Monodon		Phocoena	
ame	H. rostratus	M.bidens	M.bidens	M.bidens	P.gangeticus	M.monoceros	M.monoceros	P.phocoena	P.communis
useum	E.U.A.	E.U.A.	R.S.	E.U.A.	E.U.A.	I.M.	E.U.A.	R.S.	W.R.U.
umber	C.H.r.2	C.Me.S3	C,30-33	C.Me.S2	C.Pl.G2	M.gal.	C.Mo.M17	C,13	B 274
ex	Female	Male		Male	Female				
ge	young			adult		young	adult		
.									
.									
.									
.	+	+	R	+	R	+	+	R	+
.	B	+	R	+	- to B	B?	+	- to B	-
.	+	+	+	+ or nil	+ or nil	nil	+	+	+?
.	B-	B	+	+ or nil	- to B	nil	+	- to B	-
.									
.									
.	-	+	+	+	-	nil	+	-	-
.	-	-	nil	+ or nil	nil	nil	+	nil	-
.	-	+	+	+	B	nil	+	B	-
.	-	-	nil	+ or nil	nil	nil	+	ct. or nil	-
.					bones of manus emb. in ct.	see text		see text	see tex

In the following account references have been made and diagrams borrowed from Turner's Marine Mammals[85] :-

MYSTACOCETI.

Manus tetradactyle except in Balaena.

8 skeletons studied, all in EUA (Table No.89)

Family BALAENIDAE.

Genus Balaena.

2 specimens studied.

In B. mysticetus (C.B.m.1), there was fusion of eps. 3 & 5
" B. mysticetus (C.B.M.24) " " " " " 3 & 5

The manus was set in plaster.

Family BALAENOPTERIDAE.

Genus Balaenoptera.

6 skeletons studied (Table No.89)

B. rostrata

In these animals carpus, metacarpus and phalanges are embedded in cartilage and form a triangular flipper.

In skel. C. Bpt. r.1 there was fusion of eps. 3 & 5

NOTE: Epiphysis for proximal radius was represented by a cartilaginous covering only, under which the diaphysis was seen sprouting proximally. Ep. for proximal ulna was similar but it was partly ossified.

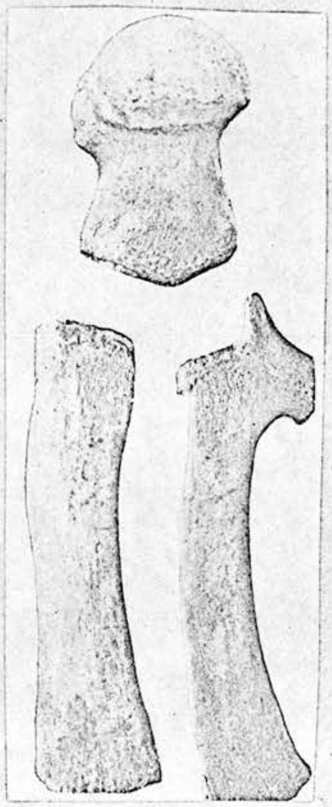
In skel. C. Bpt. r.2 there was further fusion of eps. 4,9,11

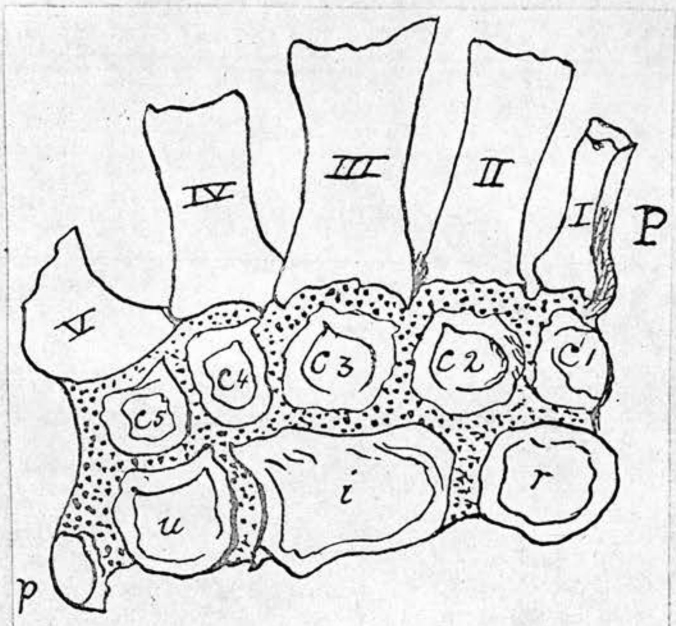
NOTE: There was slight ossification in the cartilage covering distal ends of radius and ulna in the same way as in proximal ulna of the previous specimen.

Table No. 91

Order: CETACEA Sub-Order: Odontoceti

Fam.	D e l p h i n i d a e							
Genus	Phocoena		Cephalorhynchus	Globiocephalus	Grampus	Lagenorhynchus	Delphinus	
Name	P. communis	P. communis	Electra clancula	G. macrorhynchus	G. griseus	L. albirostris	D. delphis	D. delphis
Museum	E.U.A.	R.S.	E.U.A.	E.U.A.	E.U.A.	E.U.A.	E.U.A.	E.U.Z.
Number	L27LXII	C,29	C.Crh.a.1	C.Gl.mac.1	C.Gr.g.1	C.Lgh.al.1	C.D.d.2	KK 39.3
Sex					Male	Female	Male	
Age					young	adult	young	adult
	+	+	?	+	+	+	+	+
	B?	+	?	+	B	+	B	+
	+	bits	?	+	+	+	+ (bits)	+
	B	B	?	* +	B?	B+	B	+
	B?	-	-	+	+	+	+	+
	-	-	-	**B+	B?	B+	B?	+
	B?	-	-	+	+	+	+	+
	-	-	-	**B+	B?	B+	B?	+
		sk.varnished		*eburnated				
	ep. both ends of Mc's and Ph's, stage '-'		manus imperfect	**bone formation in plate, different in texture from shaft			ep. both ends Mc & Ph '-'	arm, forearm & manus bones fused Mc & Ph embedded in ct.
	$\frac{24-25}{23-23}$		$\frac{27}{26}$				$\frac{50}{51}$	
	All h o m o d o n t							





Hyperoodon. Manus.
r, i, u, proximal carpals ; *p*, pisiform ; c_1 to c_5, distal carpals ; I to V, metacarpals ; P, pollex.

Fig. 59.

Balaenoptera sibbaldi. Adult bones of arm and fore-arm shown. (from Turner's 'Marine Mammals', plate IV p.48).

Fig. 60.

Diagram showing arrangement of bones in the carpus and the metacarpals of Hyperoodon (from Marine Mammals).

B. borealis

In skel. C. Bpt. b.1 there was fusion of eps. 3 & 5

NOTE: Eps. 10 & 12 in the same condition as described in specimen, C. Bpt. r.2

B. sibbaldi (Fig.59).

In skel. Bpt. s.25,f there was fusion of ep. 3. Manus missing.

NOTE: No epiphysial centre in distal ends of humerus, radius and ulna.

In skel. Bpt. s.22,f there was fusion of eps. 3,4,5,6,9,11

NOTE: Both ends of metacarpals and phalanges were rough and tipped with cartilage which bore no trace of ossification. Distal radius and ulna were covered with cartilage in which ossification was noticed. Fig.59 shows how the epiphyses appear when ossified and fused completely at the proximal ends of humerus, radius and ulna and at the distal end of humerus. The figure does not show epiphysial fusion at distal ends of radius and ulna.

B. musculus

In skel. C. Bpt. m.9,m there was fusion of eps. 3,4,5,6,9,11

NOTE: Distal ends of radius and ulna and carpals were fixed in a mass of cartilage. Their epiphyses were definitely ossified but were lagging in fusion.

O D O N T O C E T I.

Manus always pentadactyle.

26 specimens studied. (Tables Nos.90 & 91).

Family PHYSETERIDAE.

Sub-Family Physeterinae.

Genus Hyperoodon.

In skel. H. rostratus,f,EUA,C.H.r.2, there was fusion of eps. 3 & 5

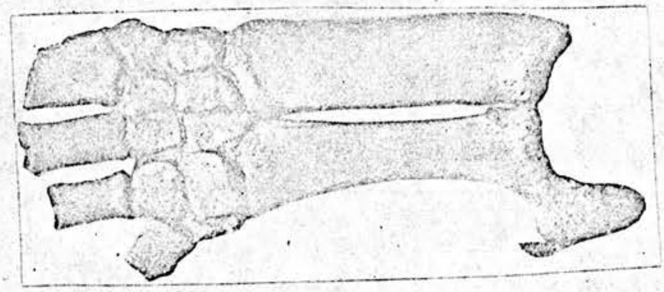


Fig. 61.

Pectoral limb of Mesoplodon bidens.
(from Marine Mammals p. 90)

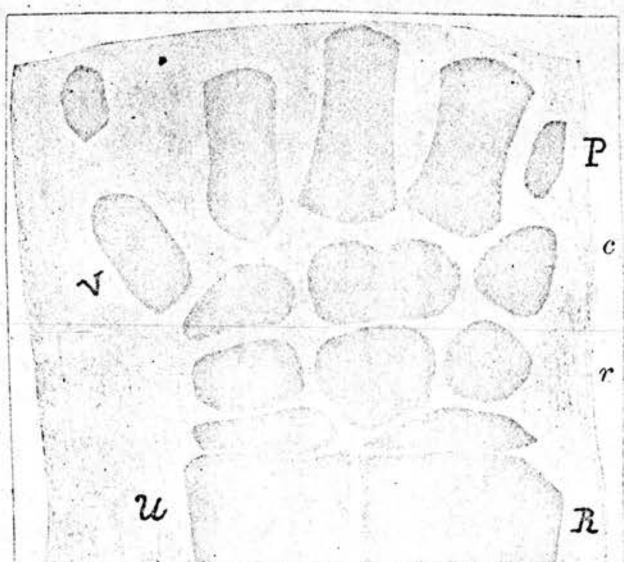
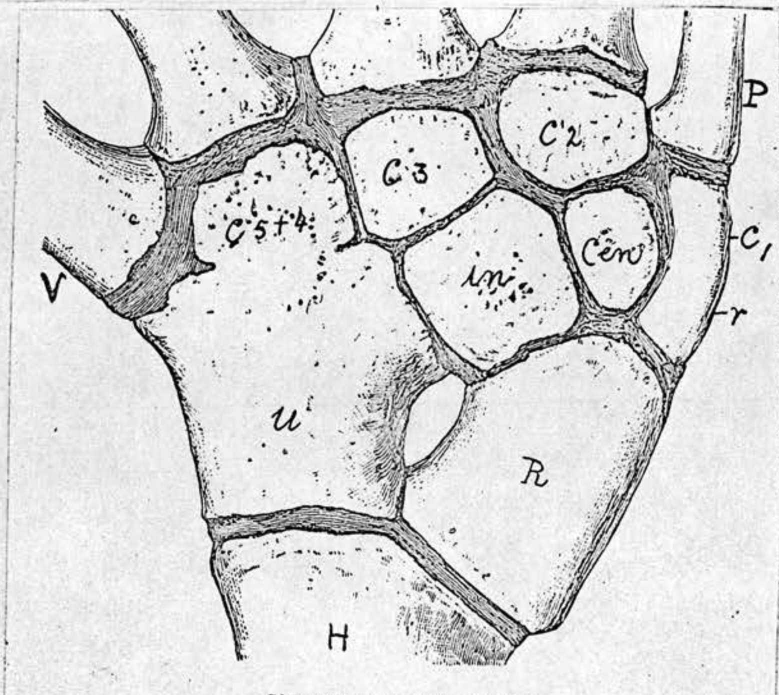


Fig. 62.

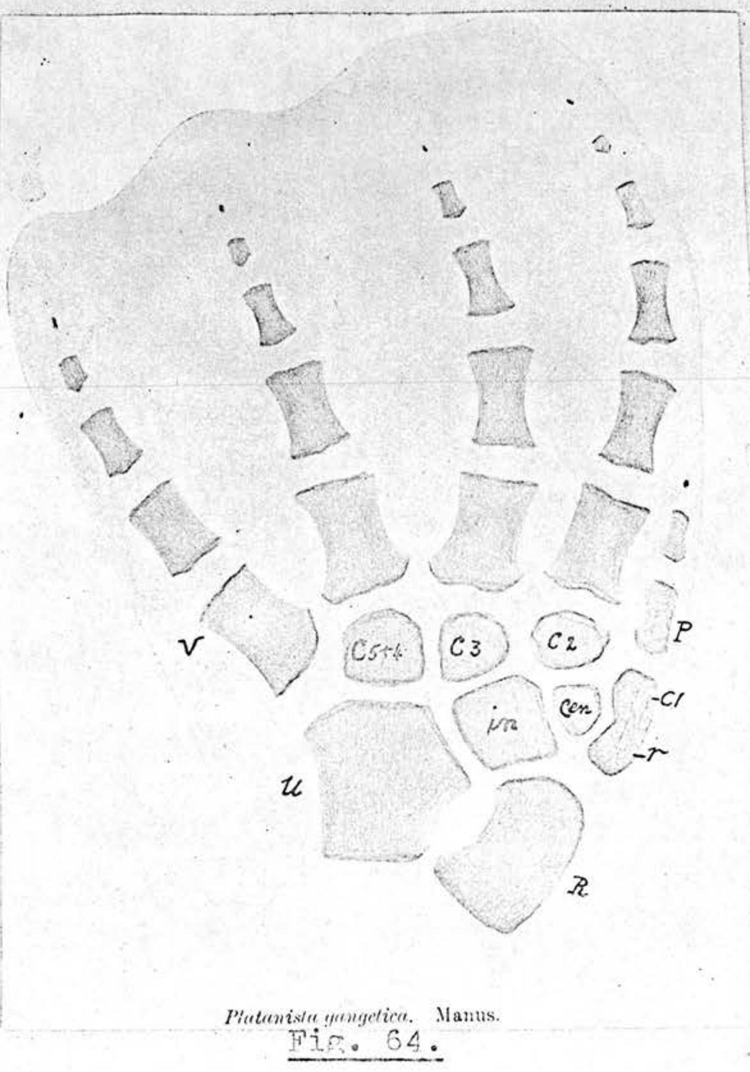
Carpo-metacarpal region of M. bidens.

(from Marine Mammals p. 90).



Platanista gangetica. Manus.

Fig. 63.



Platanista gangetica. Manus.

Fig. 64.

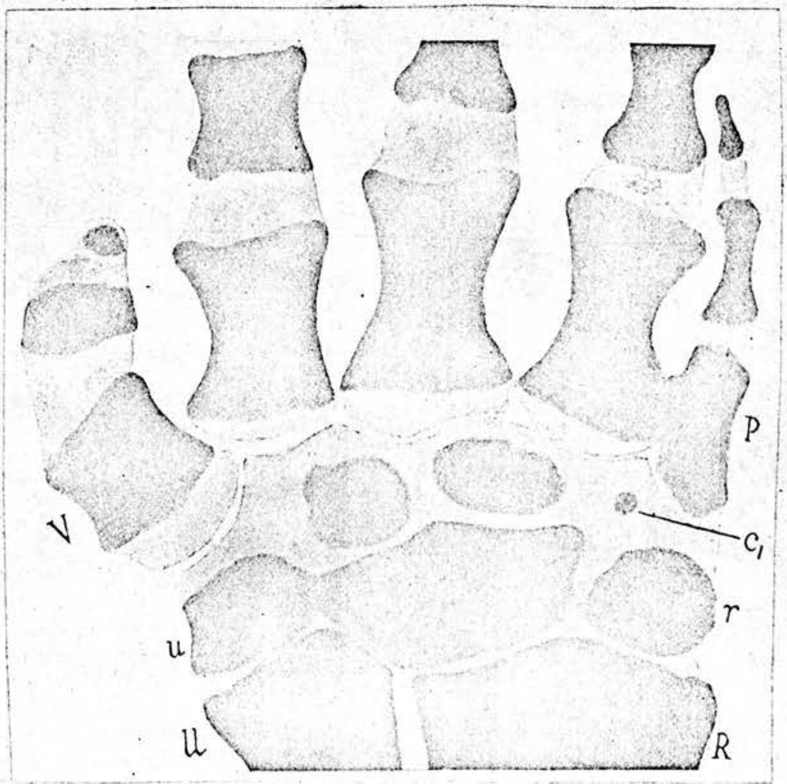


Fig. 65.

Figure showing manus of Monodon monoceros. Radiale, r; ulnare, u; first and fifth metacarpals, p & V respectively; distal carpalia, C_1; radius, R; ulna, U. Phalanges imperfect.
(from Marine Mammals).

NOTE: Epiphysis for epicondyles not seen. In manus, carpals and metacarpals were embedded in a mass of cartilage. Phalanges absent (Fig. 60).

Genus Mesoplodon.

3 specimens studied. (Figs. 61 & 62).

In skel. M. bidens, EUA,C.Me. s.3, fusion of eps.3,4,5, 9,11

" " " " ,m, EUA,C.Me. s.2) further fusion of eps.6?,
& RS, C30 to 33) 10?, 12? (ossification
) doubtful)

Family PLATANISTIDAE.

Freshwater cetacea. Pectoral limbs broad, truncated at free end (Fig. 63).

4 skeletons of P. gangetica studied (EUA, C. Pl. g.1,m and 2,f; IM, m.g,f and s.m.g). Their radii and ulnae looked very much alike (Fig.64). All epiphyses, except proximal humerus, were cartilaginous. The bones were embedded in a mass of cartilage. Elements of proximal humeral epiphysis (ep. 3) were fused in one of the skeletons studied at the Indian Museum and complete fusion of proximal epiphysis with shaft of humerus was seen in the other.

Family DELPHINIDAE.

Dolphins.

Genus Monodon.

3 skeletons studied. (Fig. 65).

In skel. M. monoceros, IM,m.g, fusion of ep. 3

" " " EUA,C.Mo. m.17) further fusion of
& EUA,C.Mo. m.18) eps. 4,5,6,9,10,11,12

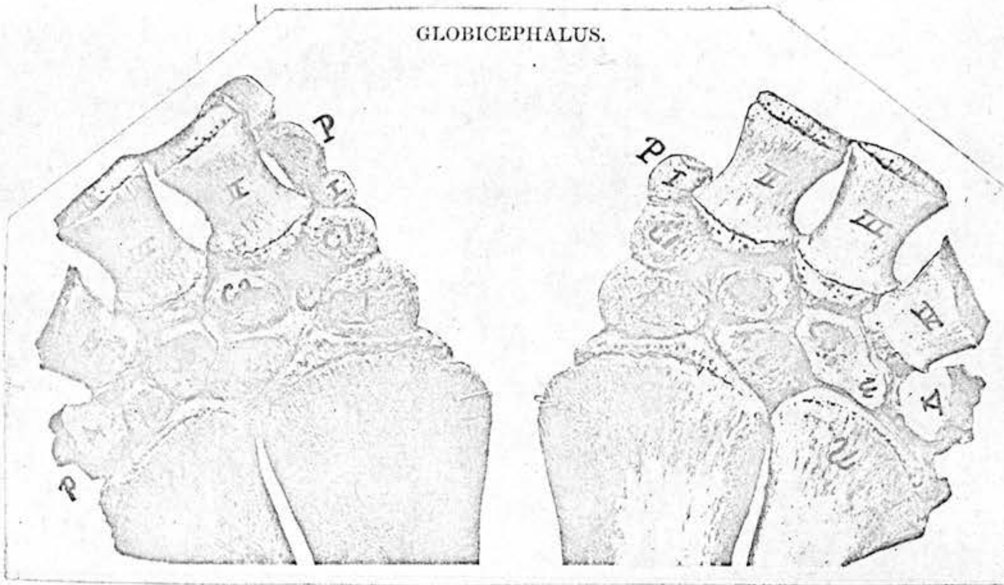


Fig. 66.
Pair of articulated limbs of an adult Globicephalus melas (from Turner's Marine Mammals).

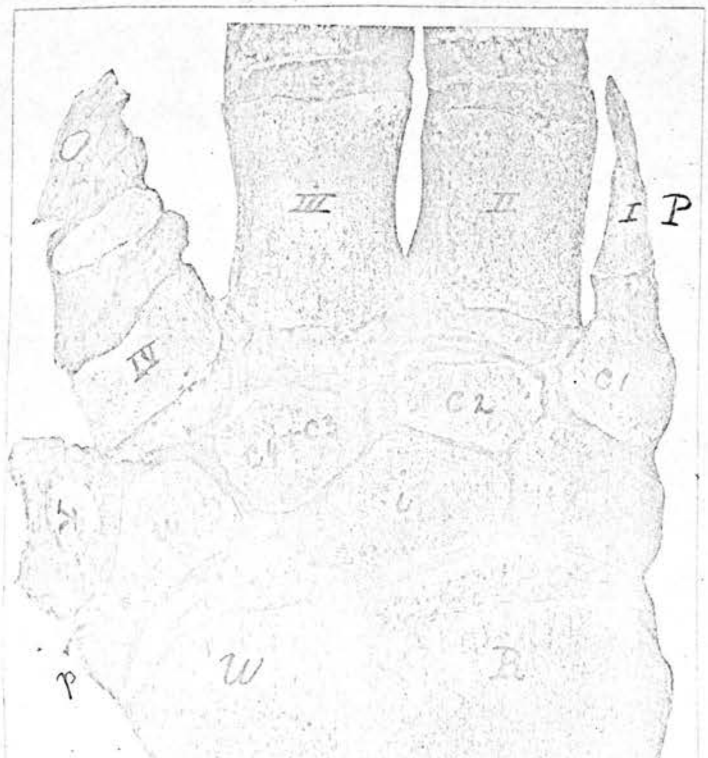


Fig. 67.
Dorsal surface of left manus of a Grampus griseus. Fifth digit rudimentary.
(from Marine Mammals).

Fig. 68.
Dorsal surface of right manus of a Delphinus delphis. (Marine Mammals).

Genus Delphinapterus.

In skel. D. leucas EUA,Dpt.1.3, all ep. for humerus, radius and ulna were fused.

Genus Phocaena.

Porpoise.

P. communis or Phocaena - 4 skeletons studied.

In skel.	RS, C13		fusion of eps. 5,3 (R)
" "	WRU, B274 & EUA, L27,LXII)	) further	" " ep. 3
" "	RS, C29	"	" " " 4

NOTE: Diaphyses and epiphyses of all bones of pectoral limbs were embedded in cartilage.

Genus Cephalorhynchus.

Only 1 specimen studied, C. albifrons (Electra clancula), EUA, C. Crh, a.l. All epiphyses in cartilage.

Genus Globiocephalus.

3 skeletons studied. (Fig. 66).

In skel.	G. melas, EUA,Gl.m,21,	all ep. in cartilage.
" "	G. macrorhynchus, EUA,Gl.mac,1	fusion of eps. 3,4,5, 6,9,10,11,12
" "	G. indicus,f, IM,m.g.	fusion of eps. 3 & 4

NOTE: No trace of other epiphyses; they were probably ossified from shaft. Epiphyses seen at both ends of metacarpals.

Genus Grampus.

Pectoral limbs narrow, falcate.

2 specimens studied. (Fig. 67)

In skel. G.griseus,m, EUA, Gr. g.1, fusion of eps. 3,5,9,11

" " " EUA, Gr. g.15, further fusion of eps. 4,6,10,12;

Genus Lagenorhynchus.

2 specimens studied.

In skel. L.acutus,f,EUA,C.Lrh.ac,1, fusion of eps. 3,5? (bits of bone fused, gaps occupied by cartilage), 9,11

" " L.albirostris,f,EUA, C.Lrh.all, fusion of eps. 3,4,5, 9,11

Genus Delphinus.

2 specimens studied. (Fig. 68).

In skel. D.delphis, EUA, D.d.2, fusion of eps. 3,5?,9,11; rest same as in skel. C.Lrh.ac 1

" " " EUZ,KK,39.3, fusion of eps. 3,4,5,6,9,10, 11,12

DISCUSSION:

In the 34 skeletons studied above, it was amply brought out that there was no joint cavity proper in the pectoral limb except at the shoulder, all shafts and ends of bones being fixed in a mass of cartilage and fibrous tissue. This arrangement, as said before, is the result of the pectoral limbs being chiefly balancing organs and not prehensile. The epiphyses, except at the proximal end of humerus, have therefore undergone regressive changes. Growth in length of bones is carried on, as in non-epiphysial parts, through ossification from metaphysis without appearance of a separate centre in the cartilage representing the epiphysis; or an epiphysial centre appears in an irregular fashion or in bits and proceeds liesurely with ossification; or there is "lapsed union" which is such a common feature in aquatic animals. It is hardly possible to prepare a schedule of union for these epiphyses. An approximate order has been presented in the accompanying Epiphysial Chart (Fig.69) and below:-

Elements of proximal & distal ep., humerus
Proximal epiphysis, humerus
Proximal epiphyses, radius and ulna
Distal epiphysis, humerus
Distal radius and ulna

Distal radius and distal ulna very often do not have any bony epiphysis. Proximal radius and ulna, and distal humerus occasionally miss the same. Proximal humerus being the only epiphysis which functions in a more or less active manner, as in land animals, observes a regular fusion schedule. Its position in the fusion list is, therefore, reversed as compared with land animals. The position of distal radius and ulna, however, remains constant.

GENERAL OBSERVATIONS ON EPIPHYSIAL FUSION.

In the foregoing pages has been described epiphysial fusion as far as it could be gathered from the material available for this study. Intricate problems cropped up at every step, for the proper solution of which a much wider assortment of skeletal specimens was indicated. The hypotheses given here are, for the most part, tentative, as they could not be tested in all cases against the right type of material.

Stevenson, and Todd and his school visualised a picture of epiphysial fusion which would be a standard mammalian characteristic. Since on land, all mammals are supposed to have started as quadrupeds it is not difficult to conceive of a homogeneity of fusion, if there were no other factor to disturb or modify their pose or poise at rest or in motion. From their birth to their maturity, however, animals differ widely between themselves in their body-limb proportions, habitat, habits of procuring food and instincts of avoiding danger and self-preservation. These differences acting for millions of years have implanted on their bony and other structural developments a pattern that has become a genetic factor. In taking to new environments again, for millions of years, the genetic factors also have undergone more or less alterations and offer to the observer a mixed picture of the original characters and the later modifications that appeared in an uncertain fashion. This leads to the difficulty which one has often to meet with in unravelling the complications that a particular study may present and have actually presented in the previous pages.

An uncomplicated study may be supposed to start from what the biologists have termed a 'generalised type' of land mammals with no special adaptation. Its near relatives may show a change of habits and habitat without a corresponding modification in bony and epiphysunion picture. Its distant relatives will perhaps show more striking changes in environments and morphology, and the epiphysunion picture will show greater divergence.

The question of adaptation to surroundings and its reaction on epiphysial picture is therefore one of paramount importance. If adaptation to a change of surroundings for a sufficiently long time brings in a change in the picture of epiphysial fusion and morphology, then it stands to reason that animals evolving in widely different manners but conforming in habits and habitat should show similar anatomical features and epiphysunion configuration, i.e., they will show a convergence in these respects.

If only a section of this hypothesis can be proved, then the conception of Stevenson, Todd and others has to be given a good-bye and that of biologists, viz: the adaptiveness to environments and convergence of characters, will stand.

In the foregoing accounts, epiphysial charts, figures and graphs, the present study has shown that no single epiphysunion picture can speak for all groups of animals as the sole unalterable pattern in every detail. Every group has its own "Group-Pattern" which may be widely different from others. Even the same group represents the end of so many different influences that have acted on its members that to analyse them involves endless difficulties. For instance, the epiphysial fusion in man as a species, represented graphically (Fig. 9) shows three types of sequence on Stevenson's scale.

Type I. Shows no or slight variation from Stevenson's schedule.

(a) The works of Lewis & Flecker completely agree.

(b) The works of Gray & Todd show that the sequence varies slightly in the fusion corresponding to the First Phase in generalised mammals. (p.60).

(c) Shows slight variation in the Second Phase as may be noticed in the works of Piersol, Sidhom & Derry and Basu & Basu.

Type II. Involves variation in both Phases (Krause, Frazer, Poirier, Morris, Cunningham 1922, Dixon).

Type III. Shows sequences with larger variations.

(a) Shows agreement with Stevenson's schedule at the start of fusion but divergence in subsequent behaviour (Dwight, Terry, Bryce, Henle, Hepworth, Holmes & Ruggles, Engelbach & McMahon).

(b) Shows total disagreement (Gegenbaur, Cunningham 1937, Davies & Parsons, Paterson, Galstaun).

This reminds one of the fact that nature's efforts to evolve any particular type of organ or animal have passed, as testified by embryologists, through repeated trials and failures, adaptations and modifications, and rejections and restorations. An analysis of these will naturally lead to complicated results.

As distinguished from the hypothesis of Stevenson, Todd etc., the present work has resulted in bringing out that epiphysial fusion pattern more or less follows the adaptations of the physical needs of the animal to its habits and surroundings. The pattern will not show much difference from the ancestral one, if the adaptation has been a recent one and has not succeeded in securing deep morphological changes. Whether or not very subtle differences based on minute difference in the pattern of fusion of epiphyses in limb-bones as compared to those in the trunk may be utilised in building up a specific, generic or familial pattern in any Order of mammals is much too large for the scope of the present work. It may however be mentioned that Todd[31], after prolonged assertions of the uniformity of epiphysial fusion in all animals, had in his own last work on "Epiphysial Union in Mammals with special reference to Rodentia" failed to establish his theme even in Rodentia. This has been partly shown in pp. 114 to 116 & 123 to 127 of the present work.

The diaphysio-epiphysial junction has been supposed in this study to be a weak point in the structure of a long bone. Sufficient strain may cause, according to Surgeons, a separation at the plane of junction. It has also been assumed that from the beginning ('B') of epiphysial union starts a process of consolidation of this junction that reaches its culmination in total fusion (+).

Before proceeding to deal with these fusions, it must be presumed that the factors involved in indicating 'priority' of fusion in the epiphyses are two-fold; (1) the nature of the epiphyses and (2) the 'essentiality' of the neighbouring joint to the economy of the animal. In regard to the nature of epiphyses , only terminal phalanges and articular epiphyses are considered. The traction epiphyses may be presumed to be in the nature of sesamoid bones, as in medial epicondyle and olecranon seen in Chiroptera (p. 216); or they may be considered to be the vestiges of separate bones incorporated with another e.g., the sternal ossicle representing suprasternal bone ossified near or with sternal end of clavicle (Dawson[28] & Todd et al[31]), or at lateral end of clavicle, as in Pedetes kaffer, RS, C27 (p. 118). Nonarticular epiphyses like proximal ulna may be similarly ignored. Proximal fibula, according to Stevenson, is uncertain in its behaviour, especially in man. It may therefore be left out of consideration.

In regard to essentiality, the terminal phalanges usually obtain 'high priority', since in progression they have to dig into the ground or branches of trees and secure for the limb the friction or reaction necessary to overcome gravity. Other phalanges follow sooner or later. But where the limbs have been partially relieved of prehensility, e.g. in the prehensile-tailed new-world monkey Cebinae and Mycetinae, this priority will be forfeited and other epiphyses will come up to take this position.

Meanwhile, almost equally essential in pulling the body forwards and in prehensile acts, namely, the elbow joint involving the distal epiphyses of humerus and the proximal radius, is wrangling with terminal phalanges for priority, and is often successful in occupying an earlier position in the fusion scale. For instance, the distal epiphysis of humerus fuses earlier than terminal phalanges in Lemurinae, Nyctipithecinae, Cebinae, Cercopithecidae, Anthropomorphidae etc.; the proximal radius fuses earlier in Semnopithecinae, Simia and all scansorial animals. Epicondyles of humerus and olecranon do not figure so much in this picture as they do not contribute any articular surface.

For a well co-ordinated and balanced progression on four limbs, it is equally important that the act of pulling forwards of the body be supplemented by pushing or lunging the same forwards. This is achieved by (1) the lifting force of calf muscles exerted at the calcaneal epiphysis and acting on the ankle as the fulcrum, and (2)the extensors of the hip acting on the thigh. Hence distal tibia and fibula and proximal femur loom large as the next in importance to terminal phalanges and elbow. With the consolidation of these the animal has entered one end of all its bony levers into strong fulcral systems. Epiphysial cartilages at the other ends of such bones are free to continue their activity and add to the length of the bone and to that of the limb, so that there may be mathematical adjustment between the body-limb proportion of the animals and the use required of their limbs. This brings to a close the first stage of epiphysial fusion and, in small animals, it is very quickly attained.

The completion of fusion of metapodia (metacarpals and metatarsals) and phalanges other than terminal may have occurred within this period or may lag along with tardy fusion either at hip or at ankle. In larger animals this tardy period may be looked upon as 'puberty' (see p.166), the first stage mentioned above being then called 'childhood or juvenility'.

There may be a comparatively long pause during which there is no further attempt of the remaining limb epiphyses to fuse, though general physical maturity of the body may have been arrived at by this time. In animals like rodents, the urge to completion of fusionsof epiphyses at knee, shoulder and wrist is very slow and it has been questioned (Dawson[79]) whether they are ever attained at the wrist of captive rodents.

The 'adult period' is ushered in by fusion of the remaining epiphyses. Not much stress should be laid on a particular sequence being universal in animals even of the same species, for once any one of the late-fusing epiphyses has started uniting others follow suit, and it is unimportant which of them fuses earlier or later; for, fusion now is a question of firm consolidation, the main function of production of new bone at the site of epiphysial cartilage having been completed when the epiphysis started fusing with the diaphysis ('B' stage; Todd et al[31]). The only principle to be borne in mind is that epiphyses round knee, wrist and shoulder are usually the last to fuse.

The discrepancies that have often been met with in the previous study were at times due to many of the skeletons having been collected from menageric or captive animals, where nutrition had suffered and captivity told upon the metabolism and equilibrium of the body tissues (Todd et al[31]).

For the purpose of a review of epiphysial fusion, a start may be made from what is observed in terrestrial mammals of a 'generalised' type having no special adaptation to a particular habitat or mode of life. The order of fusion in Centetidae is taken as the standard, since it corresponds so closely with the order given by Stevenson and since, in bony configuration and habitat, the members of this family show no specialisation.

The epiphyses of their long bones fuse in two phases in the following order:-

First Phase (juvenility & puberty)	Terminal phalanges	
	Distal humerus	(elbow)
	Middle phalanges	
	Proximal phalanges	
	Proximal radius	(elbow)
	Head femur	(hip)
	Metatarsals Metacarpals	(metapodia)
	Distal tibia; distal fibula	(ankle)
Second Phase (adolescence)	Proximal tibia; proximal fibula Distal femur	(knee)
	Distal radius; distal ulna	(wrist)
	Proximal humerus	(shoulder)

The insectivore Erinaceidae (except the natatorial Hylomys, p.53) has the same order of fusion. Hystricomorpha (Rodentia, p.123), according to Todd, shows no variation in the first phase, though in the present work, epiphysis distal humerus fuses earlier than terminal phalanges. In the second phase, both observations show slight acceleration of fusion of distal femoral and proximal humeral epiphyses over their immediate predecessors in the Centetidae scale. Fusion in Camelidae and Suidae (Ungulata, p.158) and Caprinae (p.155) is also similar, except that fusion of proximal radial epiphysis immediately follows terminal phalangeal, and distal tibial and fibular precede femoral head, features which are common to all Artiodactyles. The second phase in these families is characterised by the knee (eps. 21 & 22) being preceded by the wrist (distal radius & distal ulna; eps. 10,12). Tapiridae shows fusion earlier at ankle than at hip. Proboscidea, representing terrestrial progression per se and having peculiar vertical limbs, shows earlier fusion of head radius, probably as a result of the enormous weight being thrown directly over it. It also shows a gradual fusion of members of metacarpus and metatarsus (metapodia) extending over a wide range of time - starting to fuse along with head radius and finishing just before closure of epiphyses at hip and elbow. But it should be noted that earlier fusion of metapodia than the standard is also seen in Hystricomorpha. The second phase of fusion in Proboscidae is remarkably like that in Centetidae. Procavia (Hyracoidea) shows a general retardation of phalanges and metapodia, its proximal phalanx pes fusing after head femur and distal tibia and fibula.

Myrmecophagus is the member of an Order which is believed by comparative anatomists to have evolved from a different stem of Eutherian mammals than the rest. Whether this has any bearing on the epiphysial picture is not known. But the fusion of its distal humeral epiphysis is retarded to a position even later than those of all phalanges and proximal radius, thus approaching a condition seen in its relatives, the arboreal Sloths and Tamandua.

Whatever slight variation or alteration in position may occur in the fusion schedule of the terrestrial families considered above, the underlying principle of fusion in two stages - the first involving fusion of epiphyses of manus and pes and those about elbow and shoulder, and the second concerned with fusion round knee, wrist and shoulder - is not deviated from. This may be taken as laying the foundation of the 'Theory of Convergence' as applied to epiphysial fusion in animals that differ widely in zoological classification but conform in methods of progression.

The following adaptations to habitat may now be taken up and an attempt made to see how far the theory of

Convergence may be applied to epiphysial fusion in each case.

Cursorial
Predatory and Saltatorial
Arboreal and Scansorial
Fossorial
Natatorial and Aquatic
Volant and Aerial

The different adaptations on land may be looked upon as connected with or evolved from the original terrestrial method of progression as follows:-

- Terrestrial
  - Arboreal
    - Scansorial
  - Cursorial
    - Predatory
    - Saltatorial
      - Offensive
      - Defensive
  - Fossorial

The peculiarities of acceleration and retardation in the cursorial and the related adaptation are shown in the annexed table (Table No.).

It will be seen that in cursorial, predatory and saltatorial adaptations there are two common features of acceleration and one of retardation with very minor exceptions.

(1) Metapodia is always accelerated except in Cervidae and Macroscelididae. It therefore consolidates at the early part of the first phase of fusion i.e., in 'juvenility'. The

TABLE NO. 92

Adaptations and Epiphysial behaviour.

Adaptation	Animal	Acceleration	Retardation
Carsorial	Simplicidentata (Rodentia)	Metapodia; dist. hum.; prox. rad.; distal tibia	Proximal femur
	Duplicidentata (Rodentia)	Metapodia; dist.tib.	Proximal femur; proximal tibia
	Bovidae (Ungulata)	Proximal radius; dist. tib.; dist. rad. & dist. ulna	Proximal femur; proximal tibia
Predatory	Cynocidea (Carnivora)	Metapodia; dist. fem.; dist. ulna & dist. radius	Distal tibia; dist. fib.
	Arctoidea (Carnivora)	Metapodia; dist. tib. & fib.; dist. rad. & dist. ulna	Proximal femur; prox. tib. in Ursidae
	Viverridae (Carnivora)	Metapodia; dist. tib. & fib.; dist. rad. & ulna	Proximal femur
	Dasyuridae (Marsupialia)	Metapodia; dist. tib. & fib.; dist. rad. & ulna	Proximal femur
Saltatorial (offensive)	Felidae (Carnivora)	Metapodia; dist. tib. & fib.	Proximal femur
Saltatorial (defensive)	Cervidae (Artiodactyla)	Dist. tib.; dist. dist. rad. & ulna	Proximal femur
	Equidae (Perissodactyla)	Metapodia; distal tibia	Proximal femur
	*Macropodidae (Marsupialia)	Metapodia; all phals. distal femur	Not observed
	Pedetidae (Rodentia)	Metapodia; dist. tib. & fib.; dist. femur	Proximal femur
	Macroscelididae (Insectivora)	Proximal humerus; dist. rad. & ulna	Proximal tibia
Fossorial	*Talpidae	Not observed	Not observed
	Chrysochloridae (Insectivora)	Proximal humerus	Dist. rad.& ulna
	*Phascolomyidae (Marsupialia)	Prox. hum.; dist. radius & ulna	Prox. fem.; dist. tibia & fibula
	*Peramelidae (Marsupialia)	All phalanges	Not observed
	Dasypodidae (Edentata)	All phals.; metapodia; prox. rad.; dist. rad. & ulna	Distal humerus
	*Orycteropodidae (Edentata)	Phalanges; metapodia	Not observed
	*Monotremata	Phalanges; metapodia	Not observed
	Myomorpha (Todd[31]) (Rodentia)	Dist. tib. & fib.; proximal humerus	Proximal femur

NOTE: Asterisk(*) indicates that the animals concerned could not be studied on skeletons of the proper stage of fusion, or the latter were obtained from animals in the juvenile or first stage of fusion.

Metapodia in Cervidae makes substantial addition to the length of the limb and hence its fusion is retarded. The Macroscelididae belongs to the generalised type of animals in the mammalian kingdom,viz: the Insectivores,and does not have much change in its epiphysial fusion.

(2) Distal radius and ulna are usually accelerated except in Rodentia. The Artiodactyla make up for their lag in Metapodia by acceleration at wrist.

(3) Retardation is commonly seen in head femur except in the predatory Cynoidea.

Since femoral head and distal tibia and fibula stand in a reversible relation as regards the fusion of their epiphyses,therefore when one is retarded the others are accelerated and vice versa. Epiphyses for distal radius and ulna and that of proximal tibia stand in similar relation, though in the analysis given in the accompanying table it could not be shown in all cases for want of specimens in the right stage of fusion. Epiphyses for distal humerus and proximal radius may also be considered in the same light.

A convergence of sequences of epiphysial fusion is, from the above analysis, noticeable in the great leapers (Saltatorial) in the fact that epiphyses at ankle (distal tibia and fibula) do always precede fusion of that at the hip (head femur). This early fusion of ankle over hip seems to be a common character of all fast animals except Cynoidea and Macroscelididae. The other characteristics viz: early fusion at wrist and/or retardation of proximal femur must be present even if there be no acceleration at ankle. According to the previous classification, therefore, epiphyses at ankle in runners and leapers fuse at late juvenility or early puberty and that at hip fuses at late puberty or early adolescence. The juvenility in all such animals is thus characterised by fusion of epiphyses of all phalanges and metapodia, distal humerus and proximal radius, the puberty by fusion of epiphyses at ankle and hip, and the adolescence by fusion of those at knee, wrist and shoulder.

Table No. 92 shows interesting examples of Convergence. The most convincing evidence of convergence (similarity) of sequences of epiphysial union is provided by those seen in animals belonging to such widely divergent stocks as Viverridae (Carnivora) and Dasyuridae (Marsupialia). The latter consists of animals with bodies and habits like the former, and the similarity extends equally to fusion sequence of their epiphyses with a small exception viz: in Dasyuridae distal ulna does not participate in the acceleration of distal radius, as is seen in Viverridae.

In Fossorial adaptation, the anatomy is profoundly changed only in moles and to a certain extent in Monotremata.

Others are not obligatory burrowers and so they do not suffer any remarkable skeletal change.

In Table No. 92 is seen certain features of epiphysial fusion in fossorial mammals. In the perfect fossorial adaptation of Chrysochloridae, as explained in pp.62 & 63, the humerus is buried in the side of the thorax and is required to be short for burrowing. This brings an early fusion of its proximal epiphysis allowing those at distal radius and ulna to unite after it. The latter are therefore comparatively retarded. In Phascolomyidae, however, the urge for producing effective short arms and forearms extends to the whole forelimb; consequently epiphyses for proximal humerus, distal radius and distal ulna fuse earlier than their predecessors in the standard scale. The picture looks as if the first phase of fusion would consist, in addition to epiphyses of whole manus and pes, those of arm and forearm as well, leaving epiphyses of thigh and leg to fuse later in the second phase. The fusion therefore is limb-linked, the first phase being linked to the forelimb and the second to the hind. The conception given under terrestrial adaptation has therefore to be modified in this case.

Peramelidae, Dasypodidae, Orycteropodidae and Monotremata show importance of early consolidation of epiphyses of paws for convenience of burrowing. Distal radius and ulna are, as in Phascolomyidae, accelerated in Dasypodidae.

Myomorpha represents animals which are more fully adapted for cursorial or terrestrial existence than fossorial. This is reflected in their skeleton which shows no fossorial modification. Their epiphysial fusion shows the following as worked out by Todd (see p. 116):-

(1) Accelerated fusion of epiphyses for metapodia, distal femur, distal tibia and distal fibula. These are cursorial features.

(2) Acceleration of proximal humerus. This is a fossorial feature.

From what has been said above, it will be realized that the principle of convergence is at work in the epiphys-union pattern of fossorial animals as well.

The <u>Arboreal</u> adaptation shows various modifications according as the animals move (i)sluggishly or (ii) fast or (iii) the efforts of its limbs are supplemented by a prehensile tail or other predatory, cursorial or other adaptation. The annexed table (No. 93) will show the conditions observed.

The arboreal Carnivora and the predatory and arboreal Marsupialia have not been included in the above table,since arboreal adaptation in these animals is secondary they being primarily cursorial and predatory animals.

TABLE NO. 93

Epiphysial behaviour in arboreal adaptation.

Animals	Acceleration.	Retardation.
UNCOMPLICATED TYPE.		
Soricade	No change from standard	No change from standard
SLOW MOVING.		
Lorisinae	"	"
Bradypodidae	"	"
FAST MOVING.		
Without adaptation		
Chimpanzee	Distal humerus	nil
Lemurinae) Galaginae)	Distal humerus; metapodia	"
Cercopithecinae	" " "	"
Chiromyidae	" ? " "	Proximal fibula
Semnopithicinae	Dist. hum.; prox. rad.; dist. rad.; dist. ulna	
*Hylobates	Dist. hum.; prox. femur	Phalanges 1
Gorilla	" " " "	Phalanges 1&2; dist. ulna
Pongo	Dist. hum.; prox. fem.; prox. rad.; prox. hum.	Phals. manus; phals. 1&2, pes; dist. rad. & ulna
Sciuromorpha (Todd)	Metapodia; dist. fem.; proximal humerus	
Myrmecophagidae	Phalanges; metapodia	Distal humerus
Tupaiidae	" "	" "
Didelphyidae	Metapodia	Proximal radius
With adaptation		
Prehensile tail		
Mycetinae	?	Phalanges? metapodia (extreme)
Cebinae	Dist. hum.; prox. rad.; dist. tib. & fib.; proximal femur	All phalanges; metapodia
Nyctipithecinae	Dist. hum.; prox. rad.; proximal femur	All phalanges; metapodia
Hapalidae	Dist. hum., prox. rad.; proximal femur	Phals. 1&2, manus; phal. 1, pes; metapodia
Long hind limbs		
*Tree kangaroo	All phalanges; metapodia; proximal femur	
Flying membrane		
Phalangerinae	All phals.; metapodia; dist. tibia & fibula	Distal humerus; proximal radius
*Galaeopithecinae	All phals.; metapodia	Distal humerus; proximal radius
*Anomaluridae	Not observed	

NOTE: Asterisk (*) indicates that the animals concerned could not be studied on skeletons of the proper stage of fusion, or they were obtained from juvenile animals.

From an inspection of the annexed table it may be seen that animals with long digits capable of grasping branches of trees invariably show early maturation of distal humerus. Proximal radius and head femur are occasional accompaniments. Metapodia is accelerated in Lemuridae, Chiromyidae and Semnopithecinae. In the freely tree-frequenting great apes the phalanges tend to be retarded. In those that have claws and do not have long digits, the phalanges and metapodia are the earliest to fuse. Hence distal humerus and proximal radius suffer comparative retardation in these animals. The reason for this state of affairs is that while in animals with long digits the latter (digits) must be allowed to continue growth as long as possible in order that they may get a better grasp on the branches of tree, in clawed creatures, the epiphyses of paws must be consolidated early to allow them to dig home their claws into or get sufficient friction by pressure against branches of trees.

In the specially adapted arboreal animals, the prehensile tail releases the urge for fusion on the epiphyses of manus and pes (see pp. 77 to 79) and there is extreme retardation of fusion of metapodia with or without that in phalangeal epiphyses. In the accompanying table is shown a graded removal of the urge according as the prehensility becomes less and less marked from Mycetinae to Hapalidae.

The original need for early fusion of distal humerus is seen in all these cases along with fusion of proximal radius and head femur and in one extreme case (Cebinae) distal tibia and fibula also join in the acceleration owing to a corresponding extreme retardation of epiphyses of paws.

Provision of a flying membrane does not very much alter the fusion schedule; for the animals examined show early maturation of all epiphyses for paws (and distal tibia and fibula in Phalangerinae) as in their relatives with no flying appendages. Hence, they all have a comparative retardation of fusion of epiphysis of distal humerus and proximal radius. In Anomaluridae there is no change from the related Squirrels. In the tree-kangaroos, the fusion is the same as in other kangaroos, except that proximal humerus is accelerated.

Regarding the Volant adaptation, the marsupials (Phalangerinae), the rodents (Anomaluridae) and the Insectivores (Galaeopithecinae), have a number of forms which are assisted in jumping by a kind of parachute, which consists of a cutaneous expansion, the patagium, stretched between the limbs on each side. The animals however are purely arboreal and the possession of a flying membrane does not assist them in attaining higher levels but is of use in floating from tree to tree or in breaking the fall while coming down. Hence, as seen before, their epiphysial fusion does not differ much from their arboreal relatives without patagium. But in the purely volant form, the bats, the patagium is a real flying organ or wing. In the fusion of their epiphysis is seen acceleration of metatarsals, proximal tibia, distal femur and proximal humerus. Retardation is seen in distal radius and ulna and very markedly in phalanges 1 & 2 of manus and in metacarpals. The retardation in epiphyses of manus is in response to the need for allowing growth in length as long as possible so that the dimensions of the wing may be increased. The proximal humerus has to consolidate early so that, along with the already consolidated distal end, the humerus may form a strong rod to act as a pivot for the flapping wing. As explained previously, great strain is felt in flying at the dorsally turned knee and the fusion of epiphyses adjacent to it is accelerated. The whole picture of epiphysial fusion in this animal, tells the story of its adaptation to physical needs.

The Aquatic adaptations may be divided into (1) Natatorial adaptations for securing food or running away from enemies by occasional swimming and (2) True aquatic adaptations in which the animal has made water its natural home. In natatorial adaptation the animal has acquired some external modifications, like webbing of the toes or flattening and shortening of the tail, without much change in bony or epiphysial pattern. In the annexed table

TABLE No. 94

Epiphysial behaviour in aquatic and aerial an...

Animal	Acceleration	Retardation
NATATORIAL.		
*Hylomys & Potamogalidae (Insectivora)	Distal tibia & fibula	Proximal femur
*Hydromys (Rodentia)	Not observed	Phalanges & metatarsals
*Hydrochoerus (Rodentia)	Proximal radius	Metapodia
*Lutrinae (Carnivora)	Not observed	Not observed
*Hyomoschus (Artiodactyla)	Proximal humerus	" "
AQUATIC.		
Otariidae (Eared seal)	Proximal humerus; distal ulna; proximal fibula	Phals. 1&2, metatarsals; distal tibia & fibula
Trichechidae (Walrus)	Proximal humerus; dist. femur; proximal tibia & fibula	Phals. 1&2, metapodia; all distal tibia & fibula
Phocidae (earless seal)	Proximal humerus	Phals. 1&2, pes metatarsals; distal tibia & fibula
Sirenia	" "	Dist. hum.; metacarpals; phalanges
Cetacea	" "	Distal humerus
AERIAL.		
Chiroptera	" "	Phals. 1&2, manus; metacarpals; distal tibia & fibula

NOTE: Asterisk (*) indicates that the animals concerned could not be studied on skeletons of the proper stage of fusion, or the latter were obtained from juvenile animals.

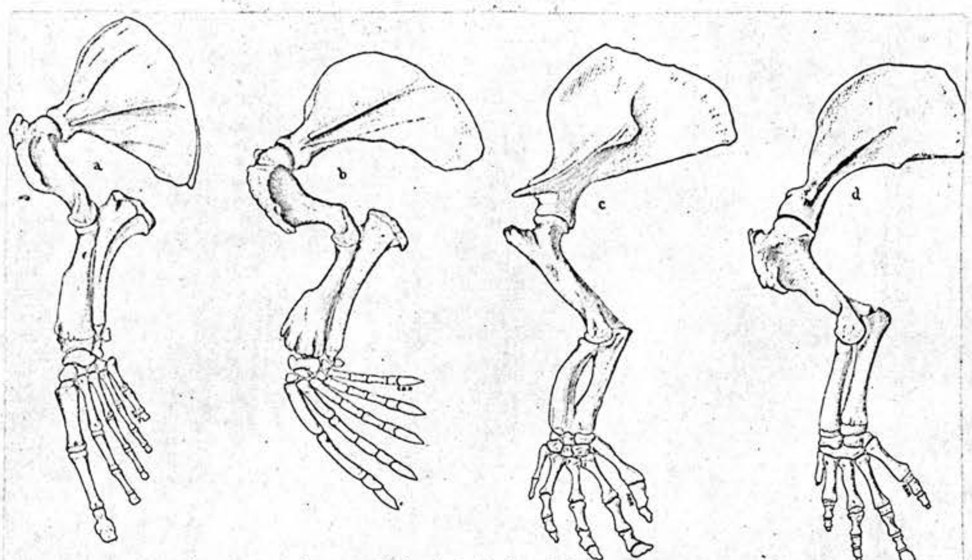


FIGURE 35. Left pectoral limbs of pinnipeds and sirenians: (*a*) sea-lion (*Zalophus*); (*b*) seal (*Phoca*); (*c*) manati (*Trichechus*); and (*d*) dugong (*Halicore*).

Figures showing the pectoral limbs in Pinnipedia and Sirenia. Note the normal number of phalanges and metacarpals. The joints are well formed.
(from Aquatic Mammals by A.B.Howell).

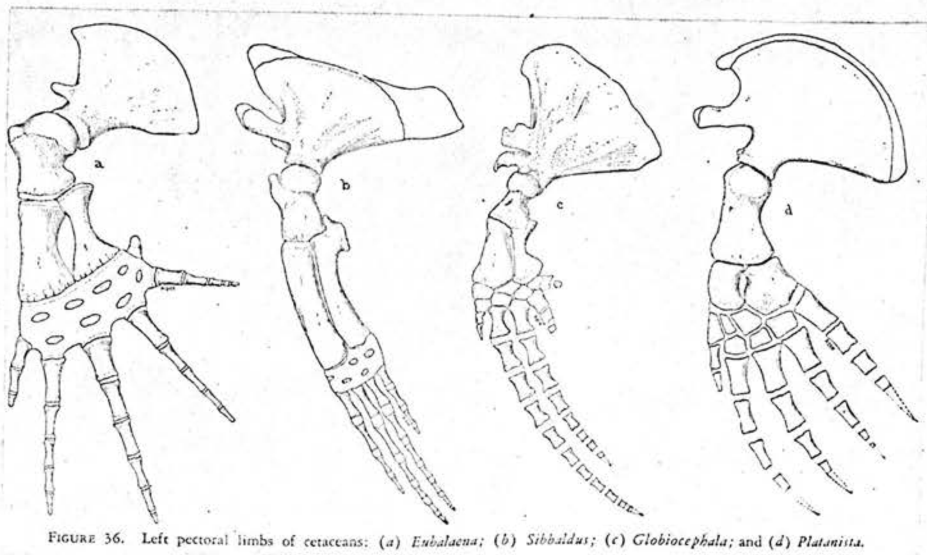


FIGURE 36. Left pectoral limbs of cetaceans: (*a*) *Eubalaena;* (*b*) *Sibbaldus;* (*c*) *Globiocephala;* and (*d*) *Platanista.*

Figures showing the pectoral limb in Cetacea. Note the large number of phalanges, the reduction of metacarpals, epiphyses at both ends of long bones of manus and transformation of most of the synovial joints into synchondrosis. (A.B.Howell).

(No. 94) is given the peculiarities of epiphysial fusion in natatorial and aquatic animals. It will be seen that phalanges and metapodia tend to be retarded and in some cases proximal femur joins them. Proximal radius and distal tibia and fibula tend to be accelerated. These show that due to buoyancy of water there is a loss of pressure on the epiphyses mentioned.

The truly aquatic animals show a gradation of their adaptation to water and corresponding changes in their external and internal anatomy and sequences of fusion. In form, the body changes from the quadruped eared seal and walrus to the fish-like but still 4-limbed earless seal, the 2-limbed Sirenia and the definitely fish-like Cetacea. The limbs are modified from the forwardly directed feet with webbed digits (eared seal, walrus) to the hind limbs turned back and incorporated in the same integument with tail (seals). In more advanced modification, the hind limbs are dropped. The whole front limb, covered in the same integument, forms a flipper which is moveable at all joints in Sirenia but at shoulder only in Cetacea. In the 4-limbed forms, the bones of arm and forearm and of thigh and leg are shortened; but those of metacarpals and phalanges are lengthened; increase in the number of epiphyses at metacarpals is occasionally and at phalanges very seldom seen. The fusion relations of epiphyses change as a result of loss of pressure on them due to buoyancy of the water medium in which they live. Epiphyses with 'lapsed fusion' and non-epiphysial ossification are often met with. In the most perfectly adapted form, Cetacea, the number of metacarpals tends to diminish but the number of phalanges is usually increased and may reach as many as 14 in a digit. The epiphyses of the whole limb (except proximal humerus) are in a state of degeneration. Ossific centres for the epicondyles humerus are never seen at all; those at distal humerus, radius and ulna may or may not be present; if present, they may appear in bits. Metaphysial ossification under cover of cartilage is seen at the ends of bones having no epiphysis; these appear porous when the superjacent layer of cartilage is removed. Besides, metacarpals and phalanges may present epiphyses at each end except the terminal. The whole forelimb is embedded in a mass of cartilage and there are no synovial joints except at the shoulder. A number of diagrams is appended to show the macrocospic and radiographic appearances of the flipper of Sirenians and Cetaceans.

The order of epiphysial closure in Pinnipedia has been discussed before (p.223). As foreshadowed in natatorial animals the phalangeal epiphyses are all retarded till the end of the schedule. Metapodials show more and more retardation as one proceeds from the less water adapted eared seal to the best adapted earless seal. The one feature that is common to all the three families is acceleration of proximal humerus (shoulder) and retardation of distal tibia and fibula (ankle), the latter reaching its culmination in the backwardly turned legs of Phocidae (earless seals). Acceleration of proximal humerus is also seen in Sirenia and, if comparison is allowable, in Cetacea. Hence, the main principles of the theory of Convergence in epiphysial fusion can be established in aquatic animals also.

It is curious that, in both aerial and aquatic modifications, loss of pressure on the limb bones due to buoyancy of air or water and the neutralisation of the effects of gravity should tend to produce similar results both in skeletal characters and epiphysial fusion. In both modifications the same integument covers the limbs, the same lengthening of digits of manus (manus & pes in Pinnipedia) occurs, and there is the same invariable acceleration of fusion of epiphyses of proximal humerus and retardation of those of phalanges, metapodia and distal tibia and fibula (when present). Hence, the principle of Convergence of features can be extended not only to similar environments but to convergent environments as well.

Regarding priority in fusion of epiphyses for metacarpals and metatarsals, it may be seen from the tables giving epiphysial readings that the stages in which the skeletons were obtained usually showed simultaneous fusion of metapodials. In the few skeletons where an assortment was possible, it was seen that metatarsals always took the lead in fusion in such divergent families as Erinaceidae, Hystricomorpha, Felidae, Bovidae, Macropodidae, Trichechidae, Chiroptera, Cercopithecidae and even in Man (Todd[73]). The exceptions were a single skeleton of Equidae (E. caballus, EUA, L31, XXI) and the aquatic Otariidae and Phocidae. Hence, it may be presumed that earlier fusion of metatarsals than metacarpal epiphyses in land mammals is a reliable constant characteristic.

Epiphysial fusion and other phenomena.

(1) Attempts have been made to correlate the sequence of epiphysial fusion to the eruption of teeth. For this purpose, Todd divided the skeletal age of animals into the first Molar, second Molar and third or last Molar stages. As showed in pp.94 & 95, epiphysial fusion does not run pari passu with tooth eruption sequence.

(2) Todd tried to correlate union of skull sutures, such as basilar, frontal, sagittal etc. with epiphysial union. This also was not very successful.

(3) As regards other epiphyses in the body, Todd and his associates had done a large amount of work with very variable results.

Absence of epiphyses.

It is common in lesser trochanter and terminal phalanges. In Monotremata, some rodents, elephants and various other animals epiphyses of many phalanges and metapodia were often absent. Metaphysial ossification must have, as explained by Todd, taken the place of epiphysial in these cases.

GENERAL CONCLUSIONS OF THE STUDY OF THE UNION OF EPIPHYSES IN LIMB BONES.

(1) Epiphyses of long bones of limbs are of three types; articular or pressure, traction and atavistic.

Traction epiphyses may have had similar origin as sesamoid bones, e.g., olecranon and medial epicondyle in Chiroptera; or, as in the case of the greater trochanter of femur, they might have formed one cartilaginous mass with the adjacent articular epiphyses and subsequently separated from the latter on account of functional changes. Their behaviour in fusion schedules is inconstant.

An atavistic epiphysis may exist as an ossific centre for a part that has lost a former functional importance, e.g., the 'praeclavium' existing in rodents as a separate ossicle but representing the sternal epiphysis of the clavicle or the ventral end of the pro-coracoid.

Supernumerary epiphyses may exist at proximal ends of metapodia of aquatic animals and very rarely in some terrestrials, and at distal ends of phalanges in aquatic animals. Additional centres of ossification may exist for the third trochanter of femur, deltoid tuberosity etc.

(2) Absence of separate centres of ossification in epiphyses at articular areas is often seen in phalanges and metapodia of monotremes and in many phalanges (especially in the terminal) in rodents, ungulates etc. Of non-articular

areas, similar absence is often seen in the epiphysis for lesser trochanter in ungulates and other animals, in those for epicondyles and distal end of humerus, distal radius and ulna in Cetacea etc. The proximal ends of metacarpals and metatarsals are most commonly non-epiphysial in land mammals. Growth at these ends occurs by metaphysial ossification continued from the shafts of the metapodia. It occurs in man as well.

(3) An epiphysis is separated from its diaphysis by an unossified plate of 'epiphysial cartilage' or 'diaphysial plate'. Ossific deposit in this plate marks the beginning of a process which later pervades the whole plate and establishes osseous continuity between the epiphysis and the diaphysis. This process is called epiphysial union or fusion. It is marked by four stages; stage of non-union (-), beginning union (B), recent union (R) and complete union (+). Once the epiphysial cartilage starts ossifying, the epiphysis enters into its 'B' stage of fusion and it may have either of three fates; (i) the most usual thing for it is to be completely ossified; or (ii) it may lose its urge for fusion and remain in a partially ossified condition between the epiphysis and the diaphysis, a condition known as 'lapsed union' which indicates a permanent forfeiture of the process of ossification; the unossified portion of cartilage may be absorbed and replaced by fibrous

tissue and the adjacent surfaces of epiphysis and diaphysis are glazed over; this condition is often seen in non-articular epiphyses of large animals, in some articular epiphyses of aquatic animals like Pinnipedia and Sirenia, and in gonadectomized (p. 50) or thyroidectomised animals; or (iii) the epiphysis may degenerate and the diaphysial and sealed over by bits of bone derived from the epiphysial cartilage or epiphysis.

(4) The articular epiphyses of long bones unite in a definite order which, as opposed to the theory held by Stevenson, Todd and others, is not universal in all land mammals, but which is the same in members of the same species and almost similar in members of the same genus or family. The sequence may differ in other families belonging to the same Order and also from that in members of other Orders.

(5) Two important principles seem to control the union of epiphyses;

(a) The adaptation of the animal to its surroundings requiring the use of certain portions of the limb more than or in a different way from the others;

(b) Use of a limb in a particular way for countless numbers of generations produces in the animal a genetic factor which controls the sequence of fusion in the epiphyses whether the animal lives in the same surroundings as its ancestors or has transferred itself to a newer surrounding for a few immediately preceding generations.

(6) Since sequence of fusion as conceived above is a function of habits and habitat, therefore the same habits and habitat should produce similar sequence in animals of widely divergent Orders. This has actually been observed in the preceding pages. The theory of Convergence is universally applicable to the sequence of fusion in the main articular epiphyses.

(7) Acceleration or retardation of fusion of individual epiphysis is linked to certain methods of progression, habits or habitats. Animals conforming in the latter will also agree in having acceleration or retardation in the fusion scale of their relevant epiphyses.

(8) Neither size, nor dimension, nor sex has any appreciable effect in modifying the fusion picture.

(9) Apart from what has been stated above, the only thing that can really affect fusion is the action of gravity. Neutralization of the effect of gravity in aerial or aquatic animals produces different sequences of fusion which may be explained by the buoyancy of the media in which they thrive. Fusion of epiphyses therefore is to a certain extent controlled by the reaction against resistance.

(10) It has been presumed that fusion of the epiphysis of a bone consolidates it and makes it better adapted to bear the strain imposed upon it.

(11) Fusion of epiphyses may be a continuous process or it may occur in spurts.

(12) Fusion period may be divided into two phases. The first phase includes closure of epiphyses for phalanges, distal humerus and proximal radius, proximal femur, metacarpals and metatarsals, and distal tibia and fibula. An earlier part of this phase may be termed the 'childhood or juvenility' of the animal, the later part being called 'puberty'. The second phase or 'adolescence' involves closure of the remaining epiphyses of the limb-bones.

SECTION II.

The Study of Epiphysial Fusion in relation to the Growth of Long Bones.

INTRODUCTION.

The major part of the work undertaken for the present thesis has been presented in Section I. The following pages deal mainly with a short review of the development and growth of the long bone and the role played by the epiphysis in its maturation. To develop the theme it has been found necessary to quote from various authorities and recapitulate many of the statements made in the foregoing pages.

Differentiation of a Long Bone.

The deeper parts of the undifferentiated mesenchyme in a growing limb bud condense and the early pre-cartilaginous axis is demarcated by a surface layer of cells. The axis of the limb soon acquires the appearance of embryonic cartilage, the limiting layer becoming perichondrium. The cartilaginous axis of the limb becomes segmented by gradual liquefaction and absorption of the pre-cartilage in those areas at which future joints will be situated. Cartilaginous rods are thus obtained which form the basis of the future long bone. The articular cartilage, constituting the articular surface, acquires a particular structure and life-history as a perenially proliferating, articular, hyaline cartilage. The deeper layers of the latter show active proliferation of cells lying with their long axis tangential to the articular surface. At the free surface the cells show considerable flattening and degeneration (Harris[25]).

Ossification of Long Bone.

There are two types of ossification in long bones. The first (ectochondral) occurs in the deeper layers of perichondrium (periosteum) that form a preosseous cellular substance distinct from the purely fibrous delimiting superficial layer. The second (endochondral) is seen in the deeper layers of cartilage. Immediately preceding the appearance of osseous tissue in cartilage, there is a change in its cells, the essential feature of which is a modification of chemical constitution. The unstable cellular substance at this stage has been termed 'preosseous tissue' and can be readily picked up by differential staining with toluidin blue. Within a mass of such tissue ossification appears as a point of spongy bone and gradually spreads to the ends (Todd[73]).

Bony Textures & Architecture.

When bone first appears it is spongy and lacks the specific trabecular architecture of cancellous tissue. It does not possess the Haversian systems. With spread of ossification the entire substance within the delimiting layer of periosteum rapidly becomes bony and the periphery takes on a slightly condensed form known as the compacta. Meanwhile the rest of the spongy mass develops trabeculae and becomes cancellous. The central zone loses bony character and fills with red marrow which produces blood elements. With increase in diameter of shaft the marrow cavity grows larger (vide infra). The cancellous tissue becomes greatly attenuated toward the shaft axis while it is constantly replacing the old compacts of the expanding periphery, where the deeper layers of periosteum are active in adding new bone. Growth occurs in length by production of bone under the diaphyso-epiphysial zone, where older cells of the constantly proliferating cartilage layer are replaced by bone penetrating from the cancellous substance of the shaft (vide infra).

The compacta forms a cylinder for the shaft, thickest near mid-length of the bone and thinning towards the extremities. As the bone grows, the inner spongy tissue becomes transformed into cancellous tissue of a definite architectural pattern with primary or coarse and secondary or fine trabeculae. The primary trabeculae are more stable, whereas the secondary trabeculae are easily modified and are probably in a constant state of change (Todd[73]).

Marrow in relation to Long Bone.

In diaphysis, the bony trabeculae are at first interspersed with blood vessels and rich red marrow. Fat gradually accumulates in droplets and the trabeculae give place to a marrow cavity. Gradually there is a patch of fat in the mid-length of the bone extending toward both extremities. In man, the fatty change progresses more rapidly in bones of forearm and leg than in humerus and femur.

In epiphysis, similar changes appear as in the shaft, but bone trabeculae are not absorbed. In man, much fat appears by puberty in epiphyses of limb bones except in proximal ends of humerus and femur where the fatty change is completed by 19 or 20 years. These changes closely parallel the dates of fusion of epiphyses except in upper femur (Todd[73]).

Ossification of the epiphysis.

Every long bone has an epiphysis at each end. the march of ossification from shaft may cease some distance from the articular surface with the production of a typical diaphysio-epiphysial plane and a vigorous ossification centre in the cartilaginous cap which is ultimately completely penetrated from this centre and united to the shaft. Imperfect restriction of diaphysial penetration is illustrated by the lower end of the humerus, especially in man. The outer end of the clavicle in man is a site where epiphysial ossification is quite meagre and is almost entirely replaced by penetration from shaft. The bases of the four outer metacarpals and metatarsals usually show no epiphysial ossification at all. Bone from the shaft penetrates almost to their articular surface (Todd[73]).

Mode of Growth of Long Bones.

Observations on the growth of long bones indicate that the relative proportions of the different parts of a fully mature bone show but little change from those as seen in its cartilaginous model. As mentioned in page 7, the growth of a bone is associated with a relativity of its form (Brash[1]).

In the diaphysis, the length, breadth and the medullary cavity all receive equal attention in the process of growth. As mentioned in pages 3 to 8, the classical experiments of Stephen Hales, Duhamel, John Hunter and others proved that interstitial growth never occurs in the diaphysis, all the additions to its length occuring at its ends by ossification of cells proliferated from epiphysial cartilage. The study of madder specimens provides direct ocular evidence of the amount of bone added at the two ends in a given time (Brash[1], Payton[10]). The increment in

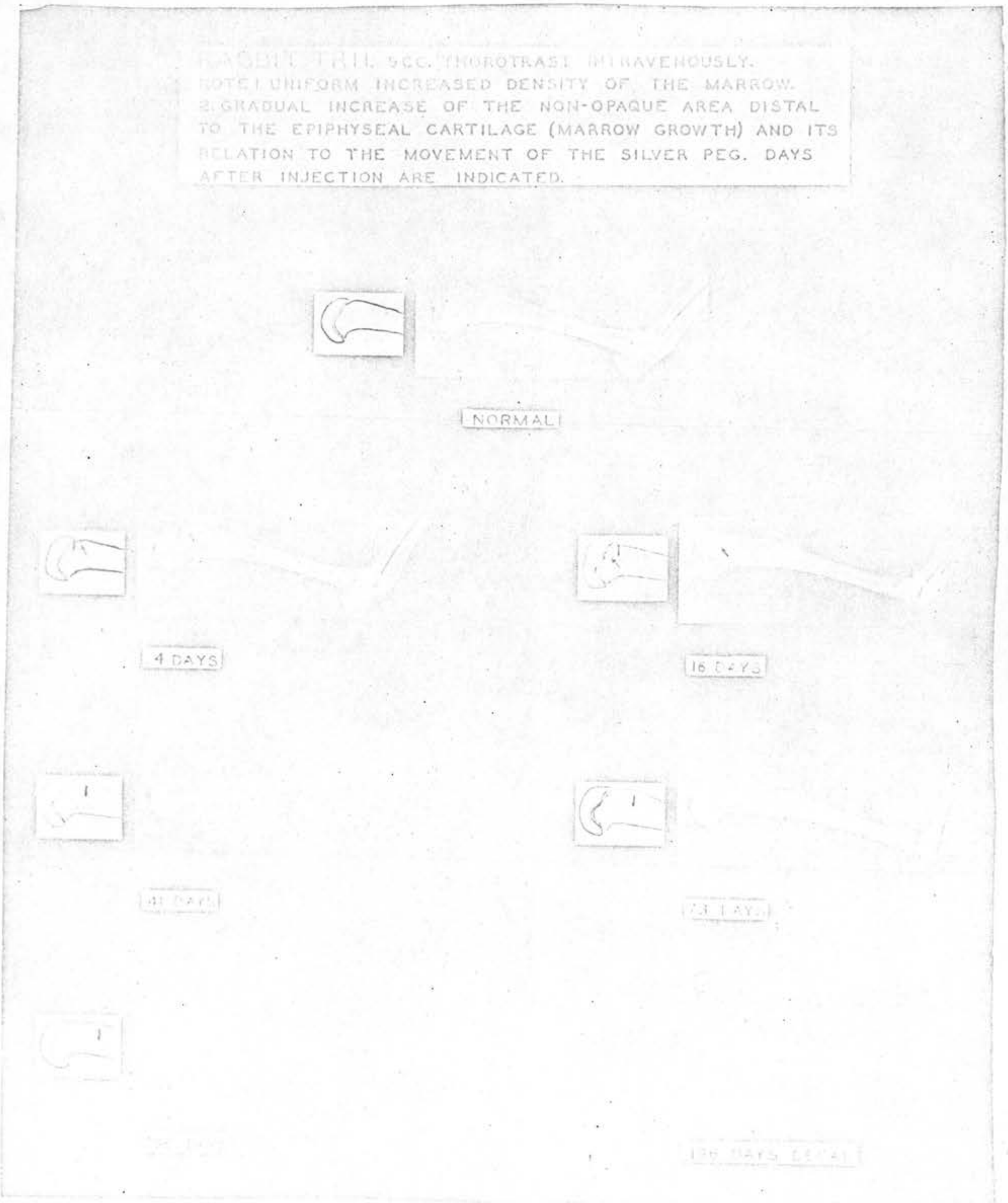


Fig. 70.

Figures showing growth in the length of the shaft of humerus in a rabbit from the adjacent epiphysial cartilage and invasion of the new bone by marrow cavity.
(Courtsey of Prof. C.A.Mortenson, Wisconsin Univ. ,U.S.A.)

width, or circumference occurs by deposition of bone at the surface underneath the periosteum. The increment in medullary cavity occurs by absorption of bone from within. Further, the new bone at the ends is canalised by marrow growth. The accompanying figures (Fig. 70) show how Mortensen[86] has demonstrated it in a Rabbit tril.

It must, however, be remembered that two phenomena are occuring side by side, whether the increment concerns the length, girth or medullary cavity of a bone. Bone accretion and absorption proceed hand-in-hand - thus resulting in a controlling effect on accretion and a total modelling effect. This has been very conclusively shown on maddered bones of pigs.

In the epiphysis, proliferation of cells from deeper layers of articular cartilage is the main factor concerned in its growth in depth. The 'diaphysial plate' (epiphysial cartilage) contributes very little to this. Payton[10] has shown that there is a faster growing epiphysis at one end of any long bone and a slower growing one at the other; that the faster growing epiphysis belongs always to that end of a diaphysis having the greater increment; and that the surface of the epiphysis next to the diaphysial plate shows marked modelling absorption.

Maddered bones may also be utilised to study their rate of growth in length and circumference and in the widening of their medullary cavity. For these studies the animal is given madder in its food for a few days or weeks and the dye is withheld for sometime before the animal is killed (indirect madder feeding). All the bone is coloured during the madder period. The bone added during the period when madder is not given in the food is seen to be free from colour. A quantitative idea of the bone added during a given period can thus be obtained. Roughened areas are seen in both the coloured and uncoloured parts of such bones; they indicate absorption of old or newly laid bone.

Payton[10] has made the following remarks on the general mode of growth in pig bones studied by him:-

> Certain fundamental processes take place in all limb bones.
>
> (1) Length is increased by additions of new bone to each end of diaphysis.
>
> (2) Breadth is increased by additions to the narrowest part of shaft.
>
> (3) Absorption process occurs immediately to the shaft side of the diaphysial new bone by means of which the latter is modified.
>
> (4) Absorption occurs within the shaft whereby the medullary cavity is increased and the tubular principle maintained upon which the shaft relies for its strength.
>
> (5) Stoppage of growth is marked by osseous union of the epiphysis, absence of new diaphysial bone formation and disappearance of the absorption process controlling diaphysial new bone.
>
> It appears also that there is a standard modelling process for each type of bone and the process is subject to gradual alterations which are also standard. Taking the humerus for example, new bone is added to the outside of the shaft in the form of a broad band which is very uniform in shape throughout the series; it constantly extends higher up on the medial side where the head of the bone owing to its mass would otherwise tend to bend the shaft.

The Maturation in Growth of a Bone.

A bone grows in length till a time is reached when the epiphysis fuses with the diaphysis and further growth in length is stopped. What initiates this fusion need not be speculated upon (pp. 16 to 21). It will be enough to say that union of epiphyses is a significant indicator of developmental progress.

The maturation leading to union can be expressed roughly in four stages (pp. 28 to 30) as -

1. Stage of no union ('-')
2. Stage of beginning union ('B')
3. Stage of recent union ('R')
4. Stage of complete union (+)

During the period when the bone is passing through the above phases of epiphysial fusion the body with all the organs and tissues is also growing. The shaft however does not grow very much, once the stage of 'beginning union' is reached. The process in the diaphysio-epiphysial junction thereafter is limited to one of completion of the fusion initiated by the 'B' stage. The time that intervenes between the stage of beginning union and final closure is usually very short, it being about a year in man. But in rodents and in some epiphyses of ungulates (vide infra) this may be quite long. According to Dawson[79] some epiphyses, notably the proximal humerus and distal femur, never unite in rats of various strains.

According to Stevenson the phenomena of epiphysial union is one of differentiation and should not be confused with the process of growth. In man, epiphysial union in long bones is limited to the 13th to the 19th year. In rats there are two periods of epiphysial fusion separated by an interval of about two years when differentiation of persisting epiphysial lines proceeds very slowly.

Sequence of Epiphysial Fusion and Growth.

From Table No.62 (p. 167A) it may be seen that Koch has worked out a sequence of epiphysial fusion in bison which, except for distal tibia, roughly corresponds with that in the bigger limb bones of man as given by Todd. Dawson's results in rats (pp. 114 to 115) show a close similarity with Koch's work on bison as regards the bones of arm, forearm, thigh and leg only. Rat and man are born with big heads and trunks but smaller extremities. In both, post-embryonal growth is more marked in limbs than in head and trunk. In other mammals, like the ungulates, who are born with long extremities and short undeveloped trunks, post-embryonal growth is slight in extremities and is finished early; but it is considerable in trunk and goes on longer. Koch maintains that no correlation exists between growth and epiphysial union in bison, e.g., of all bones, growth of metacarpus is the first to be completed, growing no more after middle of the first year, yet union of its epiphyses takes place not earlier than the 4th year; other longer bones growing for longer period than metacarpals have an earlier epiphysial fusion. But growth of humerus, femur, radius and tibia is proportional in all years and is finished at the same time. Similarly, Green & Fekete[87] report that in mouse there are two demonstrable phases with growth coefficient higher in the first than in the second. Like bison the mouse completes its growth of metacarpals and metatarsals in an early period of its life, though actual fusion of these epiphyses occurs much later. Growth in these bones having been completed, the epiphysial cartilage lies in a dormant state for some time before starting actually to fuse.

Comparative Youth.

In the following paragraphs adolescence, growth and maturity refer to the skeleton and epiphysial fusion in long bones.

One of the most extraordinary and important characteristics of human childhood is its long duration. Not only is the human infant relatively immature at birth but its progress seems retarded beyond measure in comparison with that of other mammals. In man there are three spurts of growth before adolescence; the first is most obvious in the early months and fades at the end of a year; the second appears between 6 and 8 years and is most obvious in girls; and the third usually begins between 12 and 14 years and is equally marked in both sexes. Many animals have only one spurt in growth after birth and at the end of this they are already in the adolescent stage. Brody[91] has demonstrated that this single spurt corresponds to the third in the human series. This means that the young of such animals are born comparatively mature. The rat is a simple example. At birth its skeleton is at the stage corresponding to 9 years in man. It grows for a relatively longer time than man but the interval between its birth and puberty is shorter than in man (Donaldson[84]). The pattern of epiphysial union at birth of a guinea-pig (Zuck[80]) is equivalent to 8 human years, at 8 weeks to 12 human years and at 80 weeks to 17 human years. The sheep similarly shows a single spurt in growth. Some larger rodents, like capybara, mark an intermediate stage. A dog grows to adulthood in less than 2 years, a sheep in 3, a horse in 4, a cow in 5, a bull in 6 and a bison in 7. A gorilla of 12 months has the same development as a human child of 2½ years. Considering new-world monkeys or old-world apes and other primates it is found that all of them have marked distinction from other mammals, in that the difference in the former lies in a long duration of infancy and childhood, man showing the greatest delay.

In primates, two spurts of growth are evident, one having its maximum at about birth and rapidly diminishing in velocity, the other commencing soon after eruption of first permanent molar, lasting about two years and carrying the animal to the stage of adolescence. The first spurt is that also typical of the human baby, the second corresponds to the human second and third spurts combined. Observations of Yerkes & Yerkes[88] and Bingham[89] on the Yale colony of anthropoids (mainly chimpanzees) show that in 12 chronological months the anthropoid leaps from the 6 year human stage to the 13th year stage in man. A year later the epiphyses are in the stage of closure characteristic of 19 years in man. The anthropoid therefore does not pause in its growth as man does.

From what has been said above it is clear that birth in a relatively immature state is characteristic of higher mammals; that a long period of infancy and early childhood is a primate feature; and that prolonged pre-adolescent and adolescent phases are the perquisite of man alone. Scammon has further demonstrated that skeletal development in man bears an intimate relationship to bodily growth.

The Relative Weight of Growing Bones.

Outhouse & Mendel[90] found a definite age influence on the length of limb bones in rats. At any body-weight these bones were longer in the slow growing, hence older, animals than in the rapidly growing groups. Differentiation of immature into adult bone was found to be more closely correlated with advance in age in rats than with increase in weight. Bones of the rapidly growing animals contained more water and less inorganic matter. This is probably true of all other animals. But there may be difference in the girth, weight and mineralisation of bones of animals of the same species and epiphysial stage depending on heredity, nutrition, environments etc. Bulk cuts no significant feature in studies of development, growth and epiphysial fusion of bones (Todd[73]).

Lapsed Union.

Lapsed union at the diaphysio-epiphysial plane may be seen more or less in all animals, especially in the bulkier ones. It is very common in aquatic animals.

Dawson[92] from a study on "lapsed epiphysial union in the albino rat" concludes that only those epiphyses exhibit marked retardation or 'lapse' which normally unite relatively late in mammals, and of these, those which normally unite latest show the greatest retardation. On histological examination it is seen that there are well developed systems of fibrillae in the intercellular matrix of the persisting cartilaginous plates. The typical serrated appearance of the margins of the epiphysial plate preparatory to 'beginning union' (p. 28) disappears and the cartilage is isolated from both the epiphysial and diaphysial marrow by definite plates of lamellated bone tissue. Within the plate, the isolated cartilage shows marked differentiation and some evidence of cell proliferation. The histological pattern is evidence of direct transformation of cartilage cells into bone cells. This process may ultimately result in the obliteration of typical cartilage tissue and its replacement by an atypical bone tissue. With the regional disappearance of the cartilage, vascular extensions from the marrow invade the line of union, and this zone is then remodelled.

Effect of Endocrine Organs on Skeletal Development and Epiphysial Fusion.

TESTIS.

Removal of testes before puberty causes delay in the union of epiphyses and long bones continue to increase in

TABLE NO. 95
Epiphysial fusion and length of tibio-fibula and hip-bone in normal and castrated rats.

	Males Castrate	Males Control	Females Castrate	Females Control
Litter No.8				
Age at gonadectomy 1 d				
" " death				
Number of Eps. Nos.	nil	1	4	2
Union of Eps. Nos.	"	1,2,3,4,5	1,2,3,4,5	(1,2,3,4,5 ((1 case) (1,2,3,4,5,6 ((1 case)
Avg. length tibia in cm.		3.95	3.57	3.45
" " hip-bone in cm.		4.10	3.69	3.65
Litter No.6				
Age at gonadectomy 1 d				
" " death 101 d				
Number of animals	1	1	2	2
Union of Eps. Nos.	1,2,3,4,5	1,2,3,4,5	1,2,3,4,5	1,2,3,4,5
Avg. length tibia in cm.	3.70	4.00	3.60	3.76
" " hip-bone in cm.	3.75	4.20	3.75	3.88
Litter No.1				
Age at gonadectomy 14 d				
" " death 101 d				
Number of animals	2	2	2	2
Union of Eps. Nos.	1,2,3,5	1,2,3,5(rt) in 1 1,2,3,5 in 1	1,2,3,5 in 1 1,2,3,4,5 in 1	1,2,3,5 in 1 1,2,3,4,5 in 1
Avg. length tibia in cm.	3.61	3.76	3.55	3.41
" " hip-bone in cm.	3.71	3.90	3.61	3.55
Litter No.7				
Age at gonadectomy 14 d				
" " death 103 d				
Number of animals	2	2	2	3
Union of Eps. Nos.	1,2,3,4,5	1,2,3,4,5	1,2,3,4,5	1,3,4,5 in 1 1,2,3,4,5 in 2
Avg. length tibia in cm.	3.68	3.71	3.43	3.36
" " hip-bone in cm.	3.80	3.85	3.50	3.53

Continued...

TABLE NO. 95 (Contd.)

	Males Castrate	Males Control	Females Castrate	Females Control
Litter No.5				
Age as in litter No.6				
Number of animals	2	1	2	2
Union of Eps. Nos.	1,2,3 in 1 1,2,3,5 in 1	1,2,3,5	1,2,3,5 (rt) in 1 1,2,3,5 in 1	1,2,3
Avg. length tibia in cm.	3.65	3.60	3.49	3.35
" " hip-bone in cm.	3.73	4.00	3.61	3.60
Litter No.4				
Age at gonadectomy 45 d				
" " death 116 d				
Number of animals	3	3	2	3
Union of Eps. Nos.	1,2,3 in 1 1,2,3,5 in 1 1,2,3,4,5 in 1	1,2,3,5	1,2,3,5	1,2,3,5 in 2 1,2,3,4,5 in 1
Avg. length tibia in cm.	3.74	3.77	3.63	3.45
" " hip-bone in cm.	3.80	3.94	3.73	3.64
Litter No.2				
Age at gonadectomy 45 d				
" " death 117 d				
Number of animals	2	2	2	2
Union of Eps. Nos.	1,2,3,5	1,2,3,5	1,2,3,5	1,2,3,5
Avg. length tibia in cm.	3.79	3.94	3.63	3.54
" " hip-bone in cm.	3.88	4.15	3.70	3.71
Litter No.3				
Age at gonadectomy 45 d				
" " death 118 d				
Number of animals	2	2	1	1
Union of Eps. Nos.	1,2,3,5	1,2,3,5	1,2,3,5	1,2,3,5
Avg. length tibia in cm.	3.70	3.75	3.45	3.45
" " hip-bone in cm.	3.78	3.85	3.50	3.53

NOTE:- Epiphysis (Ep.) No.1 refers to capitellum and trochlea, 2 to proximal radius, 3 to distal tibia, 4 to calcaneal epiphysis, 5 to distal fibula and 6 to medial epicondyle.

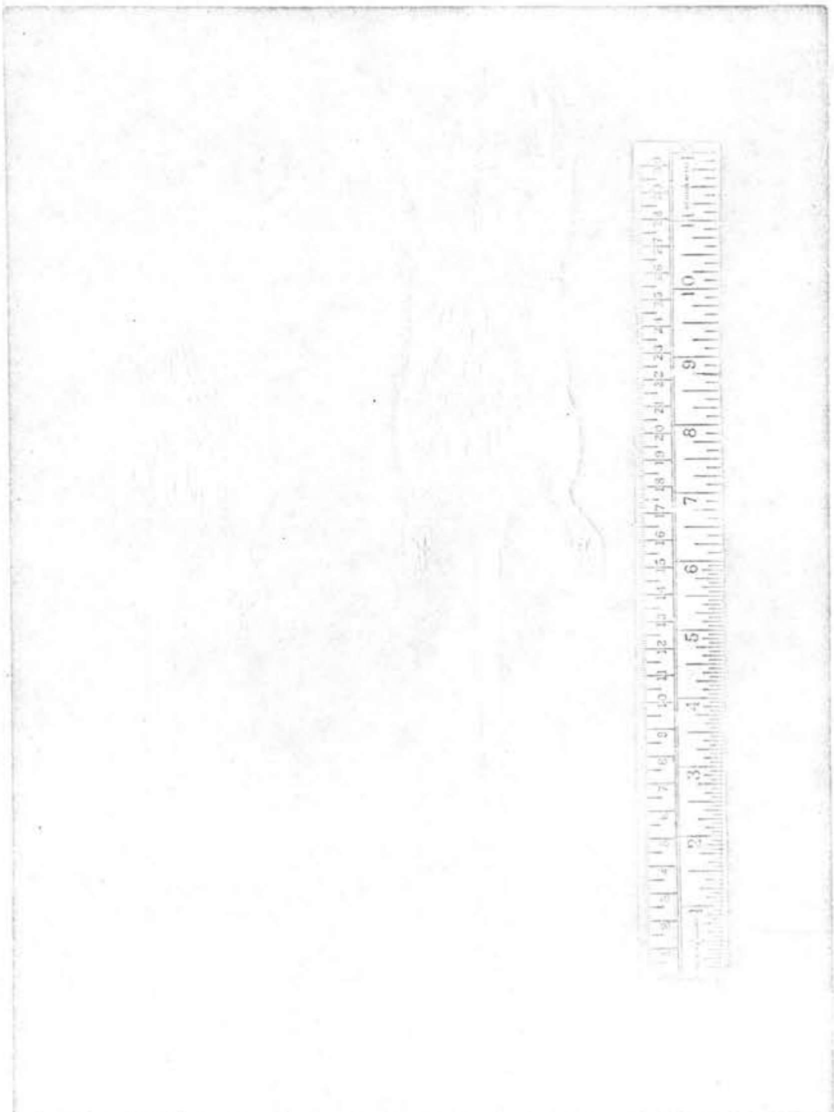


Fig. 71.
(courtsey of Dr.Y.Z.Tang).

Figure showing the gains in body length and tail length in the ovariectomized rat. The one near the ruler is the control twin, the one far from the ruler is the ovariectomized animal.

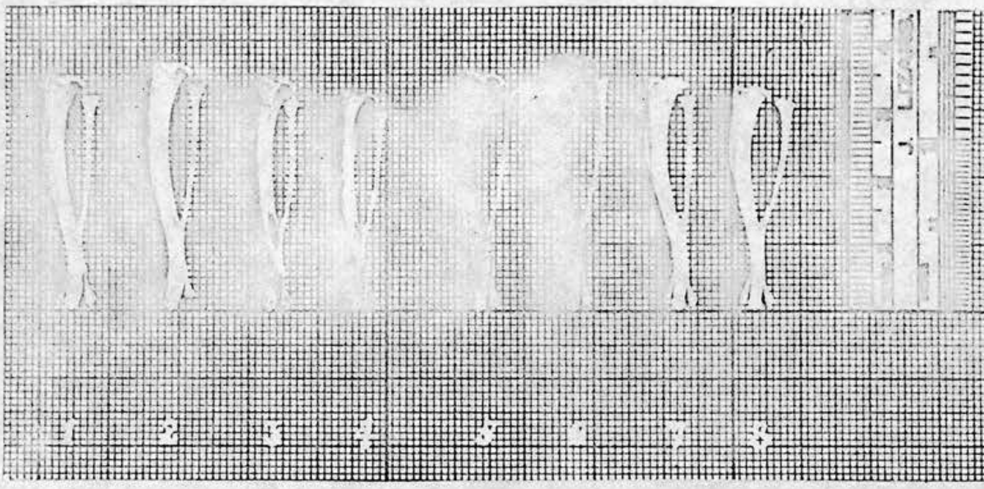


Fig. 72.

(In collaboration with Dr. Y.Z.Tang)

Figure showing changes in tibio-fibula in castrated rats. Nos. 1 & 5 are castrated males, 2 & 6 control males; 3 & 7 are ovariectomized females and 4 & 8 their controls.

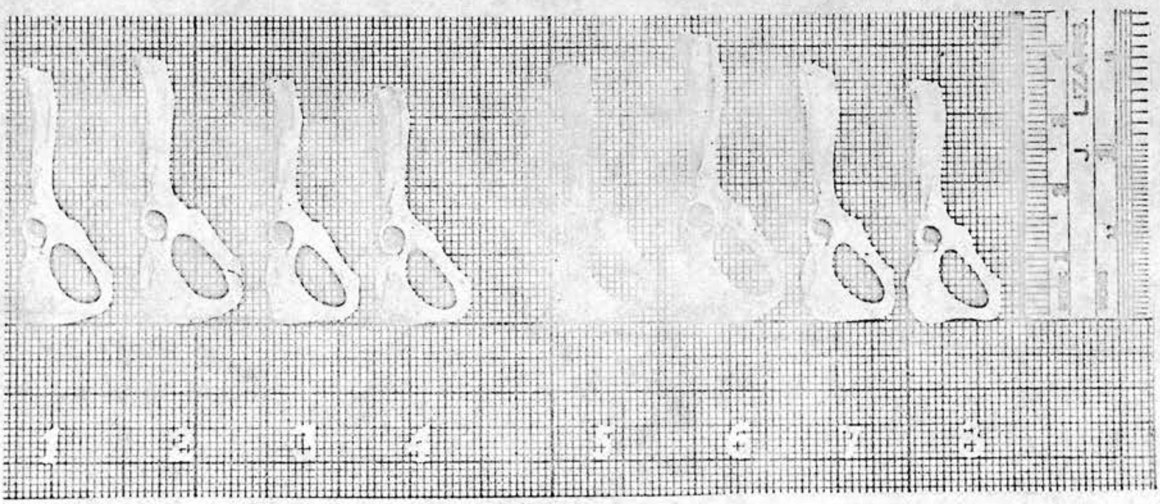


Fig. 73.

(In collaboration with Dr. Y.Z.Tang)

Figure showing changes in length of hip bone in castrated rats. Numbers are the same as in Fig. 72.

length. In man, radiographic study indicates that ossification is definitely retarded even in the later years of the second decade and epiphyses are found ununited even in the third decade of life. But there is no regular tendency to gigantism. Some animals become tall, others are short. Van Wagenen[93] maintains that castrated male rats suffer in body length, tail length, total length and body weight as compared to their normal controls.

The writer collaborated with Dr. Y. Z. Tang[42] in the skeletal assessment of 30 gonadectomized rats with 31 litter-mate normal controls. The result is shown in Table No.95. It will be found that the male castrate suffers in bone length as compared to the normal controls, whereas the female usually gains in bone length. Fig. 71 shows how the female castrate gains in body length and tail length. Figs. 72 & 73 show the changes in tibio-fibula and hip bone of male and female castrates in reference to their controls. In general, the male castrates are seen to suffer more in the above table. As regards epiphysial fusion not much significant difference was noticeable in the castrates as compared with their controls.

The writer had the unique opportunity offered to him by Prof. Brash for examining the skeleton of an Egyptian eunuch believed to be about 70 years at death. The condition seen in the skeleton has been briefly referred to in page 50.

TABLE NO.96

A Study of the Skeleton of an Eunuch.

Name of Bone	Proximal Extremity	Distal Extremity	Radiographic Appearance
Humerus	Epiphysial scar all round, seen as a faint groove at diaphyso-epiphysial junction. Compacta of outer surface of greater tubercle close to epiphysial line is deficient and extends to intertubercular sulcus. This area separates shaft from a normal area of bone formation at proximal part of the tubercle.	Normal	Proximally : appearance like loss of substance or rarefaction between articular surface and upper most limit of shaft. Distally : normal.
Radius (Rt.)	Faint epiphysial scar.	Epiphysial scar & deficient compacta at epiphysial line.	
Radius (Lt.)	No scar	do.	
Ulna	Normal	Ep. scar & deficient compacta, deepest on postero-external surface of root of styloid.	
Femur	Very faint scar round ep. line of head & gr. troch. It is deeper round lesser trochanter.	A narrow area of deficient compacta all round at ep. line, deepest over lat. & med. epiconds.	Scar round a part of head at its junction with neck.
Tibia	Sharply demarcated area of deficient compacta near ep. line, most marked on lateral and medial sides.	Marked ep. scar on medial surface of medial malleolus only. A small patch of deficient compacta near the scar.	Proximal : scar seen as 2 or 3 dense transvers lines near ep. zone. Distal: dense scar seen as 2 overlapping lines.

TABLE No.96 (Contd.)

Name of Bone	Proximal Extremity	Distal Extremity	Radiographic Appearance
Fibula	Ep. scar & deficient compacta near position of epiphysial line.	Faint epiphysial scar & deficient compacta in adjacent area.	Proximal: distinct scar as in humerus. Distal : normal.
Clavicles	Sternal end: partial union of ep. at margins. Greater portion of it. ep. missing showing failure of union. Acromial end, no ep.		Scaring & signs of partial union of ep. (lapsed union) at sternal end.

Name of Bone	Macrospic Appearance	Radiographic Appearance
Scapula	Coracoid: faint epiphysial scar at tip. Vertebral border: (1) ep. open from superior angle to apex of spine; the border is rough & longitudinally grooved; (2) ep. for inferior angle is partly fused and is partly hanging free; (3) intermediate part is normally fused. Deficiency of compacta near ep. for inferior angle. The above picture is one of 'lapsed union'.	Complete non-union of dorsal part of epiphysis for inferior angle.
Os coxae	Ilium: compacta of crest almost completely cut of from upper border of compacta of ilium. Marked deficiency on inner lip of this region. Pubis: deficiency in compacta on femoral surface from ramus to crest & tubercle. Ischium: ramal ep. shows marked deficiency of union of compact bone on outer lip especially near symphysis.	Crest shows almost complete non-union at middle third. Scar at pubic tubercle & crest. Ramal ep. shows non-union near symphysis and complete union posteriorly.
Sacrum	Bodies: disc between 1 & 2 imperfectly ossified. Lateral epiphysis : faint groove at epiphysial junction. Lapsed union is seen in many of the regions of union of the different sacral vertebrae.	

TABLE NO.96 (Contd.)

Name of Bone	Macrospic Appearance	Radiographic Appearance
Cervical vertebrae	Atlas: vertebral arches incomplete posteriorly; no posterior tubercle (lapsed union). Ep. scar at transverse process. Axis: Epiphysial scar at tip of transverse process. 4th to 7th: scars and osteo-arthritic changes on bodies.	
Thoracic vertebrae	Bodies of all vertebrae show deficient compacta at anterolateral margins. All transverse processes show more or less marked grooves at epiphysial lines; similarly at tips of spine.	Body epiphyses at 'B' or 'R' stage. Transverse processes and tips of spine show scar.
Lumbar vertebrae	Same as in Thoracic vertebrae.	
Ribs	Epiphysis head: complete or partial failure of fusion (lapsed union). Epiphysis tubercle: scar.	Union at 'B' stage. Union marked by scar.
Sternum	Incomplete longitudinal division into two unequal halves.	
Skull & face bones	All cranial sutures except basi-occipital and basi-sphenoid are open. All sutures between face bones are similarly open. Sagittal suture at obelion does not show fusion in endo- or peri-cranial aspect. Lapsed union is marked feature in sutures of skull and face.	

In Table No. 96 is given a fuller description of the bones of the eunuch.

Summary of features in the eunuch skeleton.

1. Lapsed union is characteristically present in the epiphyses which are the last to fuse, e.g., in vertebral border of scapula, neural arches of vertebrae, crest of ilium, sutures of skull and face bones.
2. Faulty bone formation near diaphyso-epiphysial junction, chiefly consisting in deficiency of compacta and partial non-union.
3. Modelling of epiphysis and shaft of long bone is unaffected.

Removal of testes after puberty does not have any marked skeletal change. Since in the eunuch skeleton described above, distal humerus escaped the stigma seen at other diaphyso-epiphysial planes, therefore the person had probably been castrated after the maturation of this epiphysis, i.e., 14.0 to 14.11 years. Since proximal radius showed the stigma to a slight degree, it may be presumed that the person had been castrated when this epiphysis was maturing, i.e., between 15.0 to 18.11 years.

In male hypogonadism, juvenile characteristics persist with extreme growth in arms and legs. The eunuch skeleton presented very long limb bones. The maximum lengths of the left limb bones and their indices were as follows;-

Humerus	35.30 cm.	Brachial index	79,89
Radius	28.20 cm.	Humero-femoral index	69.49
Femur	50.80 cm.	Crural index	87.11
Tibia	44.25 cm.	Inter-membral index	66.81

VAS DEFERENS

Tying does not result in any skeletal change.

OVARY.

Like testis, ablation of ovary results in diaphyso-epiphysial planes remaining ununited until well into the adult period.

THYROID.

Lack of thyroid secretion retards bony growth. The skeleton becomes small and stunted. The human cretin is a dwarf with short arms and legs. The dwarfism is not due to complete cessation of growth but to the failure to assume body characteristics which appear during normal growth and finally reach adult proportions. Growth takes place but the body still retains its infantile characteristics. On radiographic examination of bones of human cretins the epiphyses are seen to have been delayed in ossification and development. But they do ultimately fuse. Boetigger and Osborn[94] hold that skeletal differentiation in dwarf animals is normal in sequence, but greatly retarded in rate. For instance, at an age of 70 to 80 days, a dwarf mouse shows an epiphysial development comparable to that of normal animals 25 to 30 days old.

Reference has already been made (pp. 160-161) to the skeletons of thyroidectomized sheep obtained from the studies of Simpson[44] and Liddell[43]. In tables Nos.60 & 61 and in Fig. 41 is given the study of their long bone epiphyses. Todd, Wharton and Todd[95] studied the same material together with the records of their body weight supplied from the Cornell University. They have summarised the general results of thyroidectomy as follows:-

a. Deficient growth and modelling of the epiphyses.

When ossification is completed the epiphysis lacks character and is inadequate to cap the growing end of the shaft.

b. Defective development of age characters in epiphysis as well as in shaft.

c. Defective growth in length of the shafts.

The duration of growth is not extended but the velocity is diminished.

d. No disturbance of bone texture, weight, thickness or modelling of shaft.

Thus the locus of damage to both growth and maturation pattern is definitely and solely the diaphyso-epiphysial plane. The disturbance finds expression in a slowing but not a prohibition of developmental growth.

The pathological features of the condition are (a) irregular exuberances on shaft end resembling ossified 'proud flesh'; (b) inturned, clawed, trachoma-like epiphysial margins; and (c) a small, poorly modelled,

TABLE NO. 97

Length of Bones in millimeters (average of Rt.,Lt.).
Normal controls

No.	Sex	Age	Humerus	Radius	Ulna	Fore Cannon	Femur	Tibia	Hind Cannon
B 1125	M	14 months	160	163	203	132	190	221	139
B 1142	F	14 "	138	147	184	122	170	198	128
B 1058	F	59 "	148	155	190	128	176	204	135

Thyroidectomized sheep

No.	Sex	Age	Humerus	Radius	Ulna	Fore Cannon	Femur	Tibia	Hind Cannon
B 1887	M	9 months	124	125	154	113	143	170	119
B 1126	M	14 "	119	123	166	106	142	168	114
B 831	M	31 "	144	147	184	126	171	201	131
B 1141	F	14 "	115	114	143	104	138	156	110
B 2831*	F	22 "	124	132	161	112	147	171	119
B 1129**	F	25 "	121	126	151	109	143	168	117
B 832	F	30 "	134	138	163	119	158	190	127
B 1886	F	37 "	126	136	164	113	149	176	121
B 1059	F	59 "	125	136	166	113	150	176	120
B 844***	F	27 "	137	140	172	117	170	188	124

Epiphyses united as follows: B 1125 distal humorus and tibia, proximal radius, fore and hind cannons; B 1142 distal humerus and tibia, proximal radius, fore and hind cannons; B 1058 all limb epiphyses; B 1887 none; B 1126 none; B 1141 proximal radius; B 2831 distal humerus, proximal radius; B 1129 distal humerus, proximal radius ; B 1886 distal humerus, proximal radius; B 832 distal humerus, proximal radius; B 831 distal humerus, proximal radius, fore and hind cannons; B 1059 distal humerus, distal tibia, proximal radius, proximal ulna, proximal femur, fore and hind cannons.

*Thyroxin 0.1 mg. daily from 18 to 20 months of age.
**Delivered of small (3.5 lbs.) male lamb 3 weeks earlier.
***Not thyroidectomized but shows defective growth distal humerus, distal tibia ; proximal radius, proximal ulna, proximal femur; fore and hind cannons.

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(Modified from Todd, Wharton & Todd with corrections from observations of the writer)

TABLE NO. 97

Proportion of femur to hind cannon and of tibia to femur in percentage of length and weight (age in months)

No.	Sex	Age	EPIPHYSES UNITED		FEMUR/CANNON		TIBIA/FEMUR LENGTH
			Femur	Cannon	Length	Weight	
			Normal controls				
B 1125	M	14	No	Yes	134	269	116
B 1142	F	14	No	Yes	133	268	116
B 1058	F	59	Yes	Yes	130	306	116
			Thyroidectomized sheep				
B 1887	M	9	No	No	120	240	119
B 1126	M	14	No	No	125	261	118
B 831	M	31	No	Yes	131	263	119
B 1141	F	14	No	No	125	234	113
B 2831	F	22	No	No	124	284	116
B 1129	F	25	No	No	123	282	118
B 832	F	30	No	No	124	290	120
B 1886	F	37	No	No	123	232	118
B 1059	F	59	No	Yes	125	232	117
B 844*	F	27	No	Yes	137	245	111

*Not thyroidectomized but an example of defective growth pattern.

(Adapted from Todd, Wharton & Todd[95])

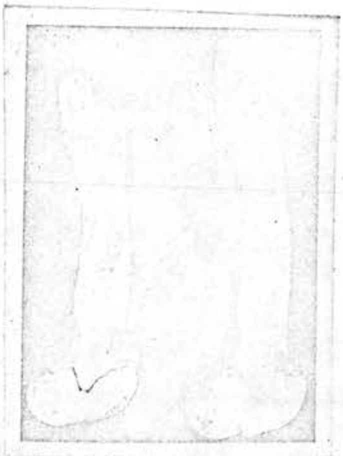

Fig. 74.
(from Todd, Wharton and Todd[95])
Right femora WRU, B1058 and B1059, twin ewes 59 months old. In the thyroidectomized twin B1059 note the irregular exuberant cauliflower-like supratrochlear surface, partial lapsed union of greater trochanter and definitely clawed, trachomatous margins to the ill-fitting lower epiphysis.

Fig. 75.
(from Todd, Wharton and Todd[95])

Right humeri WRU, B1058 and B1059, twin ewes 59 months old. In the thyroidecomized twin B1059 note the gap between head and greater tuberosity, inturned trachomatous margins of theepiphysis and the ill-fitting epiphysial cap.

ill-fitting epiphysis scarcely covering the shaft end (Figs. 74 & 75).

The following table (Table No.97) will give an idea of the retardation in length of the principal long bones with reference to epiphysial union in the thyroidectomized animals as compared to their controls. Table No.98 shows the Femur/Cannon indices of length and weight and Tibia/Femur (Crural) index in length. From a study of these tables it will be found that growth of bones has no relation whatever to date of epiphysial fusion, for identical proportions in length of femur and cannon are to be found no matter whether epiphyses are fused or not in either bone.

The direct effect of hypothyroidism is probably restricted purely to the inhibition of growth velocity, which affects the growth pattern without prolongation of the growth period.

Application of knowledge of growth studies in Cattle-rearing.

Cattle-rearing is carried on with two ends in view -

1. Improvement in various qualities in the living animal, e.g., size, docility, food utilization capacity etc.

2. Improvement of meat value.

Considerations that are important to the cattle farmer are as follows:-

1. The improvement of a sheep for mutton consists in a super-development of those parts which are largely composed of muscle. Of this improvement early maturity is the first sign (Hammond[76]). It is expressed in the skeleton by an increase in proportion of femur to cannon bone. Cannon bones and feet are devoid of meat value, while femur and, to a less extent, tibia because of the muscle around them are all important from the meat producers' point of view. The thyroidectomized sheep suffers in all these respects. It tends to have a relatively long tibia, long cannon and short femur and therefore has a poor meat value. Castration however produces long arm and leg bones. Hence meat producers in India resort so much to the castration of their goats.

2. As an animal grows older the food required for maintenance is greater. Hence the amount of gain in weight per unit of food consumed is less. Thyroidectomized animals are not economical from this point of view. Castrated animals are more economical since they grow for a longer period and fully utilize the food given to them in increasing their size and body weight.

3. Thyroidectomized animals are dull and slow. Castrated animals are active and docile. Hence castration before puberty is largely practiced in India for producing draught animals.

4. Castration of farm animals facilitates their fattening. Overgrowth and flabbiness of musculature, which mean tenderness of meat, are desired features in animals that are meant to be used as food.

ANTERIOR LOBE OF HYPOPHYSIS.

Administration of anterior hypophyseal extracts before union of epiphyses produces gigantism. The skeleton becomes larger and heavier. The response varies with sex. In males it is less marked than in females. The response is increased in both sexes by removal of gonads. There is an overstimulation of normal periosteal bone growth and intensification of activity of normal ossification zones for that period of life in which the animals are studied (Handlesman and Gordon[97]). In man deficiency of anterior hypophysis in early life results in rapid skeletal growth and abnormal tallness due to delayed epiphysial closure permitting growth of long bones to continue at an age when such growth should have ceased (Lisser[98]).

Deficiency of secretion of the gland in early life produces dwarfs. The skeleton is invariably delicate and the bones are small. The typical childhood proportions of trunk and limb lengths tend to be maintained throughout life. But congenital dwarfism in man exhibits normal epiphysial growth and fusion (Paterson[99]).

Complete removal of anterior hypophysis results in growth stasis and infantile condition. The epiphysial cartilage suffers a singular failure in proliferation, remains open and later shrinks or undergoes precocious calcification and ossification, so that further increase in the length of bones ceases (Evans[100]). Dwarfs are thus produced. Bony tissue already laid down undergoes no change.

Effect of multiple endocrine disturbances on the epiphysis in Man.

Human subjects suffering from defective hypophysis associated with a primary gonadal deficiency are often met with in whom some of the epiphyses of the long bones never unite. Radiographs of their bones show an epiphysial age which is much below their chronological age. Less pronounced cases may show more advanced epiphysial age but the lapsed diaphyso-epiphysial planes are not normal. They show the same heaped-up exuberant margins and surfaces as are found in experimental hypothyroidism (Figs. 74 & 75). A similar retardation is found in hypothyroidism and juvenile diabetes. On actual examination in radiographs, the bones show that the quiescent billowing or saw-tooth margin (p. 28) of the diaphyso-epiphysial plane has been almost entirely eroded away and replaced by a coarse exuberant cancellous bone devoid of orderly pattern (Todd[73]).

Sex in regard to epiphysial fusion.

Pryor[57], from his radiographical studies of the hands of boys and girls, was the first to draw attention to the fact that girls were more precocious in epiphysial fusion than boys. All radiologists agree that girls have an earlier fusion of their epiphyses than boys. It is not known whether this is true in the females of animals as well. Sex however does not alter the sequence or pattern of epiphysial fusion.

Epiphysial growth and fusion in disease.

The exhaustive studies of Todd has shown that acute constitutional diseases in man retard the maturation of an ossific centre, but once the cause of retardation is removed the epiphysis marches normally to its fusion and the sequence schedule is not disturbed. Similarly an acute disease occuring at the time when any epiphysis is due to unite may retard the fusion of that particular epiphysis without affecting the others. In cases of altered metabolism, there may be a general retardation of skeletal growth but there will be no specific onslaught on epiphysial growth and pattern. Similarly, disturbances in endocrine secretion, hereditary factors and environmental or nutritional changes may act on the epiphysial system en bloc without any particular bias.

In animals also the pattern of epiphysial union is not changed in gonadectomized, thyroidectomized or hypophysectomized animals. The phenomenon of lapsed union can be explained as the failure of a maximal stimulus to produce the minimal response in very tardy epiphyses, whether the stimulus is of internal origin, e.g., in endocrine disturbances, or of external origin, e.g., by loss of friction or pressure as in aquatic animals.

CONCLUSIONS OF THE STUDY OF GROWTH IN LENGTH OF LIMB BONES IN RELATION TO FUSION OF EPIPHYSES.

(1) A limb bone grows in length near its ends. It does not have any interstitial growth.

(2) Growth is seen near both articular ends, being more pronounced at one end than at the other.

(3) Proliferation of cells of cartilage at the ends of the shaft and ossification extending into them from the neighbouring bone cells are the chief phenomena concerned in this growth.

(4) The proliferating cartilaginous mass may be split up into two sections by an ossific centre appearing near the end. The portion of cartilage where the ossific centre appears is the epiphysis, limited near the joint by a layer of articular cartilage and separated from the shaft of the bone by a layer of epiphysial cartilage or diaphysial plate. Addition to the length of the epiphysis takes place by a proliferation of cells from the deeper layers of its limiting articular cartilage. Addition to the length of diaphysis takes place by proliferation of cells from the nearest layer of its limiting epiphysial cartilage.

(5) Where an ossific centre does not appear at the growing end, the articular cartilage provides the only proliferating layer and the ossification is metaphysial.

(6) Modelling absorption proceeds side by side with accretion at the outer and inner surfaces of the shaft and

at the diaphysial side of the epiphysis.

(7) Maturation of the growth of a long bone usually corresponds to the fusion of its epiphysis with diaphysis i.e., ossification of the diaphysial plate whereby the diaphysis and epiphysis become continuous; and along with this the deeper layers of articular cartilage cease proliferating. But the diaphysial plate may remain quiescent for a long time without ossifying and sometimes may not ossify at all. Such bones are considered to have completed maturation without undergoing epiphysial fusion.

(8) Once the diaphysial plate starts to fuse, maturation of the bone at the corresponding end is completed and it is a question of time before the plate completely ossifies, regresses into lapsed union or disintegrates.

(9) The epiphyses fuse in a definite sequence pattern which is roughly the same for individuals of the same species. Sex, heredity, environment or constitutional handicaps may accelerate or retard the whole sequence without altering the specific pattern.

(10) Deficiency in activity or removal of anterior hypophysis or thyroid interferes with normal growth at the diaphysial plate. The velocity of ossification is slowed down but the fusion sequence is not altered. Excessive activity of these glands overstimulates growth of epiphysial

cartilage without altering the fusion sequence. Similarly, castration has no effect on the fusion schedule.

(11) Endocrine deficiency or excess, while not producing any change in epiphysial fusion sequence, may result in distinctive changes in the growth of bones, a study of which is important from the point of view of farmers, cattle-rearers and meat producers.

(12) Finally, epiphysial fusion and growth of a bone are two overlapping phenomena which may be dissociated naturally or artificially.

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